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and Oxygen in Dormant Potato Tubers

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EFFECTS OF VARIOUS TREATMENTS ON THE CARBON DIOXIDE AND OXYGEN IN DORMANT POTATO TUBERS¹

ORA SMITH²

GENERAL PROBLEM AND LITERATURE

The marked influence of environmental conditions and treatments upon the length of the rest period of plants or plant parts is well known. Numerous investigations upon methods of abbreviating this rest period and hastening the initiation of growth have, however, failed to show convincingly the reason for the inception of this growth. Most of the previous investigations have been concerned with the changes in food reserves and enzyme activity. The present experiments deal primarily with the gaseous changes accompanying treatments which alter the rest period.

The literature of the subject frequently indicates that various outer tissues of seeds and tubers prolong the rest period by retarding the passage of carbon dioxide and oxygen. Several investigations with seeds (Crocker;⁽⁹⁾ Shull;^(26, 27, 28) Becker;⁽⁶⁾ Frietinger⁽¹³⁾) have shown that the permeability of the outer layer to gases plays an important rôle in the length of the rest period.

Studies with the potato tuber also suggest that the periderm and internal tissue may offer great resistance to the passage of carbon dioxide and oxygen and that the permeability may be changed by

¹ Paper presented to the Graduate School of the University of California in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

² Graduate Assistant in Truck Crops; resigned August 1, 1929.

various treatments. Appleman⁽¹⁾ was able to shorten the rest period of potato tubers by various treatments such as removing the skin, cutting the tubers into pieces, subjecting them to subdued light, and wrapping them in cotton saturated with hydrogen peroxide. He suggests that these treatments facilitate the entrance of oxygen into the tuber or cause it to be liberated therein. He states further: "That a great increase in oxygen absorption actually occurs is proved conclusively by the effect of the various treatments on respiration, the rate of which was determined by the amount of carbon dioxide expired from the tubers Probably under normal conditions the skin becomes suberized before the completion of some growth mechanism requiring oxygen. The rate of oxygen diffusion through the suberized skin then determines the time required for the perfection of the growth mechanism." Rosa,⁽²⁴⁾ in a study of the relation of storage humidity to dormancy of potato tubers, suggests that besides inhibiting further suberization of the skin, the moisture may also make the skin more permeable.

Bartholomew,⁽⁵⁾ in a study of blackheart in potato tubers, ascribed the injury to a deficiency of oxygen caused by the increased rate of respiration of the tissues. The available supply of oxygen diffusing inward from the surface was used up before it reached the interior tissues. He also noticed that large tubers are more susceptible to injury than small ones. Stewart and Mix⁽²⁹⁾ also showed that deficient oxygen supply, and not accumulation of carbon dioxide, is responsible for the occurrence of blackheart. Bennett and Bartholomew⁽⁸⁾ found varietal differences in susceptibility to blackheart injury. They state that these differences in behavior probably result in part from differences in permeability of the skin of the tubers to oxygen.

Magness,⁽¹⁸⁾ working with apples and potato tubers, found that the percentage of carbon dioxide of the intercellular gas increases with rise in temperature; at 22° C there was 34 per cent in potato tubers. The percentage of oxygen decreases with increase in temperature and at 22° C was found to be 5.7. Removing the peel from the ends of apples greatly decreased the percentage of carbon dioxide and increased that of oxygen.

Davis⁽¹⁰⁾ found that the ratio of carbon dioxide to oxygen in the intercellular spaces of the potato varied with the conditions of storage, such as temperature and depth of piling, and with the age of the tubers. Following storage at 17°–18° C at the end of 16 hours at 45° C in atmosphere free from carbon dioxide and rich in oxygen,

the carbon dioxide content of the interior gas of the tubers had increased from 5 or 6 per cent to 50 per cent, and the oxygen percentage had decreased from 10 or 11 to about 4.

Stieh,⁽³⁰⁾ working with potato tubers, and Johnstone,⁽¹⁵⁾ with sweet potato roots, showed that the increased rate of respiration on wounding results principally from mechanically facilitating the exchange of gases rather than from direct wound stimulation.

Wiesner and Molisch,⁽³¹⁾ using dry and moist pieces of periderm of potato tuber, found that carbon dioxide passed through the moist periderm several times faster than through the dry periderm. They conclude that gases pass through with increasing ease as additional amounts of water are absorbed by the cell wall. Loomis,⁽¹⁶⁾ in a study of the effect of humidity in storage upon the length of the rest period of potato tubers, states that at high temperatures the specimens stored in damp moss show less injury and make better growth than those stored dry. He further states that moist storage at these temperatures has no direct effect upon the rest period but probably results in more rapid formation of a wound periderm in the turgid tubers which prevents them from drying out. At moderate temperatures, however, the dry potatoes gave the best germination.

Several investigators, Shapovalov and Edson,⁽²⁵⁾ Priestley and Woffenden,⁽²²⁾ Artschwager,^(3, 4) Eames and MacDaniels,⁽¹²⁾ Rhodes,⁽²³⁾ and Herklots,⁽¹⁴⁾ have published upon the anatomy of the periderm of the potato and the conditions conducive to rapid cork formation. They generally agree that the periderm is very impermeable to water and gases and that wound periderm formation is hastened by high humidity and high temperature.

Studies on the permeability of plant membranes to water and to other liquids may also furnish evidence as to their permeability to gases, for usually the plant tissues are permeable to gases only when the latter are in solution. Palladin⁽²¹⁾ points out the difference between diffusion of gases in the dissolved and undissolved states. In the dissolved state, the condition assumed usually to occur in plants, the velocity of movement of gases is directly proportional to the coefficient of solubility of the gas in the solvent in the septum. Not all cells and cell walls, however, are impregnated with water. Livingston³ states that diffusion of dissolved gases is possible if the gas is soluble in the membrane. When the latter contains water, this kind of diffusion can occur, for the gas dissolves in water. When the membrane

³ Livingston, B. E. Footnote, in: Palladin, V. I. *Plant physiology*. 2 ed. p. 107. P. Blakiston's Son and Company, Philadelphia. 1923.

contains little or no water, but contains some such material as suberin, and the gas dissolves in this material as it does in water, the action is similar to that of a wet membrane.

Nord and Franke,⁽²⁰⁾ in a study of the mechanism of enzyme action, used tobacco leaves and found that ethylene increased the permeability of the cells.

STATEMENT OF SPECIFIC PROBLEM

Because but little is known concerning the changes in permeability to gases, in gaseous exchange, and in composition of the gases in the interior of the tubers at the time when rest is broken, the present work was undertaken as an attempt to ascertain how various treatments affect the rate of loss of carbon dioxide and absorption of oxygen, the composition of interior gas of the tubers, the permeability of the periderm to gases, and the length of the rest period.

The treatments included harvesting at various stages of maturity, subjection to ethylene chlorhydrin vapor for 24 hours, storage dry and storage moist, storage in air of high oxygen percentage, and peeling the tubers.

EXPERIMENTS ON TUBERS HARVESTED AT VARIOUS STAGES OF MATURITY

Potato tubers of the varieties White Rose and Irish Cobbler were used throughout this study. In the maturity series the tubers were of the spring crop of 1928, in the remaining experiments, tubers of the fall crop of 1928, harvested November 10. In some experiments the White Rose variety only was used. All tubers selected were as nearly free from scab and mechanical injury as it was possible to obtain. For each series of experiments the same number of tubers was selected, and they were of approximately the same size and weight.

Experimental Procedure.—Tubers of the Irish Cobbler variety were dug at five different stages during the growth of the plants: first on May 21, when the vines were dark green in color and the tubers very immature, and then, with increasing maturity, on May 31, June 11, and June 21, and on July 2, when the vines were dead and the tubers considered mature. The White Rose tubers were dug on the same dates as the Irish Cobbler, and also on July 12, when the final harvest of mature tubers was made. On each harvest date a

sample of each variety was placed in storage at 25° C. The rate of respiration of the tubers was determined at approximately two-week intervals until some time after the rest period was broken.

Rate of Respiration.—For determining the amounts of carbon dioxide given off and of oxygen absorbed by the tubers, the Orsat gas analysis apparatus was used. The closed system was followed throughout. This method was checked against the continuous flow system, ascarite being used for the absorbing agent; and only a negligible difference between the two methods appeared when the carbon dioxide in the jars in the closed system was not allowed to become higher than 4 per cent.

TABLE 1

RESPIRATION RATE OF IRISH COBBLER AND WHITE ROSE TUBERS DURING THE GROWING PERIOD AND IN STORAGE AT 25° C

Expressed as milligrams of carbon dioxide per kilogram per hour

Variety	Date dug	At time of harvest	Fourteen-day periods after harvest					
			First	Second	Third	Fourth	Fifth	Sixth
Irish Cobbler.....	May 21	31.0	9.4	4.9	4.1	5.2	4.8*	6.7*
	May 31	19.4	6.2	5.3	4.1	4.7	5.4*
	June 11	11.8	5.1	4.6	4.6	5.5*
	June 21	15.1	5.9	4.3	5.4*
	July 2	12.2	5.5	5.2*	6.0*
	May 21	37.9	12.3	8.2	6.2	6.2	4.5*	6.8*
White Rose.....	May 31	27.3	10.8	6.3	5.0	4.2*	4.9*
	June 11	22.0	8.1	5.7	4.1	5.4*
	June 21	18.9	8.1	5.8	6.4*
	July 2	13.0	7.2	5.1*	4.6*
	July 12	10.5	7.6	7.4	7.2*

* All tubers sprouted.

Glass jars of one gallon capacity were fitted with No. 14 shellacked rubber stoppers, into which were fitted one or two metal stopcocks. Wire screen platforms were placed in the bottom of each jar, and each treatment was run in duplicate. The tubers were selected for uniform size and shape, and each lot of five tubers weighed between 600 and 700 grams. At each determination a 200 cc sample of gas was drawn from each jar, and 100 cc of this was analyzed for carbon dioxide and oxygen. Carbon dioxide was absorbed by a 50 per cent solution of potassium hydroxide, and oxygen was absorbed by a similar solution, to each 100 cc of which had been added 8 grams of pyrogalllic acid. All determinations were corrected for differences in temperature and pressure, and the data are presented in terms of milligrams per kilogram per hour.

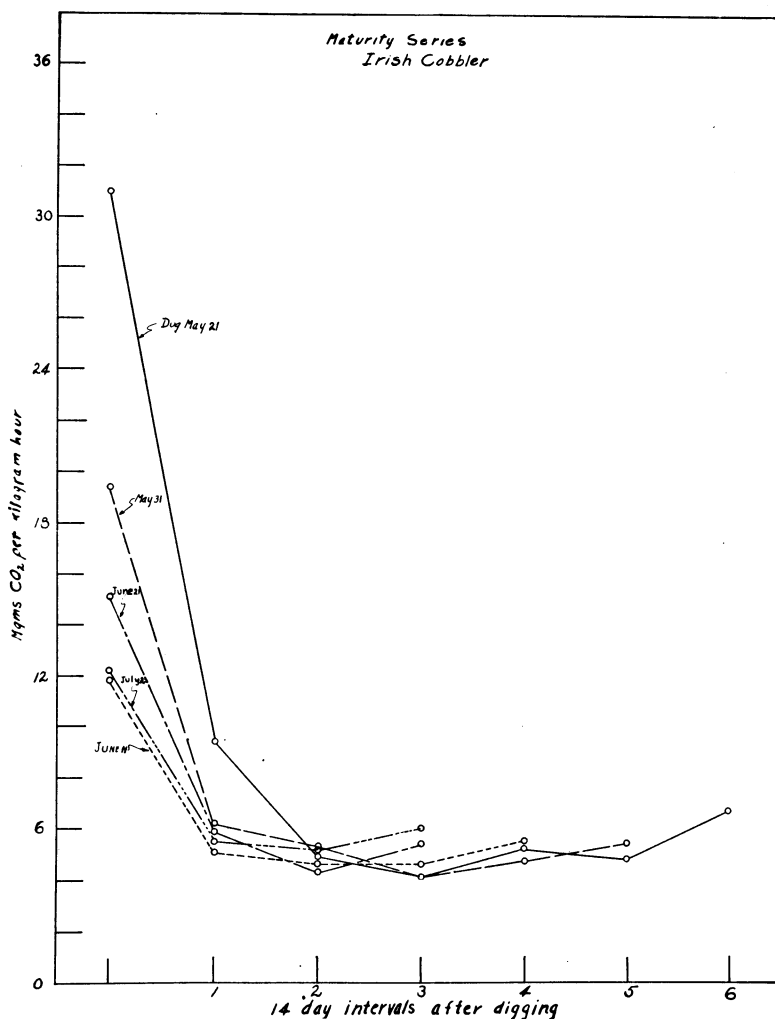


Fig. 1. Irish Cobbler tubers harvested at various stages of maturity. Respiration rates determined immediately after digging and during storage at 25° C.

Effects on Rate of Respiration.—The respiration data are presented in table 1 and shown graphically in figures 1 and 2. Respiratory activity is greatest in the earlier-harvested, less mature tubers, and gradually decreases as maturity advances. During storage also there is a gradual and regular decrease, until the respiration rates of tubers of all harvests are approximately equal at the end of the rest period. This decrease is extremely rapid immediately after harvest but diminishes during storage. The decrease in respiration rate of tubers in dry storage at 25° C is much more rapid than with those

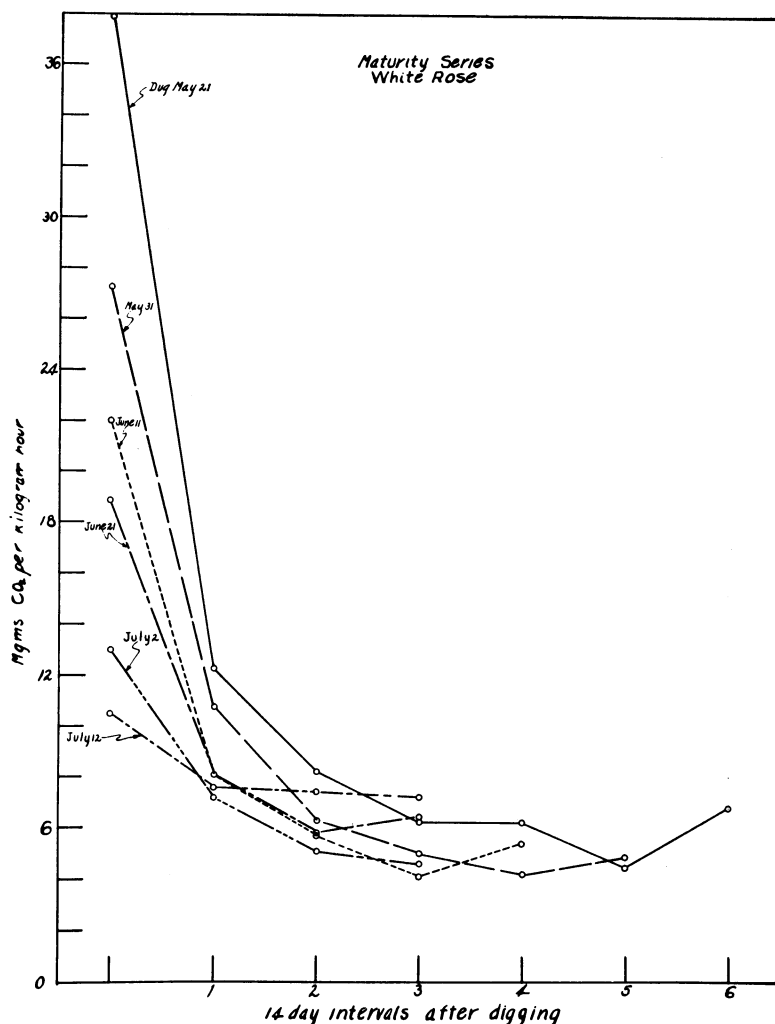


Fig. 2. White Rose tubers harvested at various stages of maturity. Respiration rates determined immediately after digging and during storage at 25° C.

that remain in the soil for the same length of time. In this respect, four to eight days in storage are equal to ten days in the soil. The rate usually increases slightly with resumption of growth. At every harvest period the White Rose tubers show greater respiratory activity than the Irish Cobbler; the former variety also has the shorter rest period. The data of table 1 also show that, with both varieties, the more mature the tuber is when harvested, the shorter is the rest period.

A COMPARISON OF WHITE ROSE AND IRISH COBBLER TUBERS UNTREATED WHEN STORED DRY AND STORED MOIST AND TREATED WITH ETHYLENE CHLORHYDRIN WHEN STORED DRY

Experimental Procedure.—Tubers of White Rose and Irish Cobbler varieties, dug November 10, were kept at 8° to 10° C until January 30, then treated and stored at 25° C to determine the differences in gaseous exchange of tubers and in composition of interior gases. The tubers were treated with 0.75 cc of 40 per cent ethylene chlorhydrin per liter of space for 24 hours, by the vapor method proposed by Denny.⁽¹¹⁾ Tubers of the dry-stored lots were stored in shallow wooden trays; those of the moist-stored lots, in wooden boxes in well-leached moist sphagnum moss or coarse, moist sawdust. The following lots of each variety were used; (1) chemically untreated, dry-stored; (2) chemically untreated, moist-stored; and (3) ethylene chlorhydrin-treated, dry-stored. The carbon dioxide given off, the oxygen absorbed, and the composition of interior gas were determined at intervals of three to seven days. The ethylene chlorhydrin vapor method, being the only chemical treatment given the tubers, will be designated throughout this paper as 'treated.' Dry storage and moist storage treatments will be referred to respectively as 'dry' and 'moist' and the chemically untreated tubers as 'untreated.'

Composition of Interior Gas.—Plugs of tissue from stem to eye end, one inch in diameter, were removed from five tubers of each lot for determination. One plug at a time was cut and pressed out of the brass borer under mercury into the gas extraction apparatus shown in figure 3. The operation of the apparatus is similar to that described by Magness.⁽¹⁸⁾ After two minutes' extraction in the Torricellian vacuum, the gas was collected in a gas burette. When samples of five tubers had been obtained, the gas was drawn into Henderson's respiratory gas analyzer (modified to have a capacity of 3.30 cc) and analyzed for carbon dioxide and oxygen. The absorbing agents for carbon dioxide and oxygen were the same as those used in the Orsat apparatus described above. These determinations were not made on the Irish Cobbler variety.

Effects on Rate of Respiration.—The Irish Cobbler untreated dry lots are, in general, higher in rate of loss of carbon dioxide and absorption of oxygen than similar lots of White Rose; with the untreated moist and the treated dry-stored lots, however, the reverse is true of

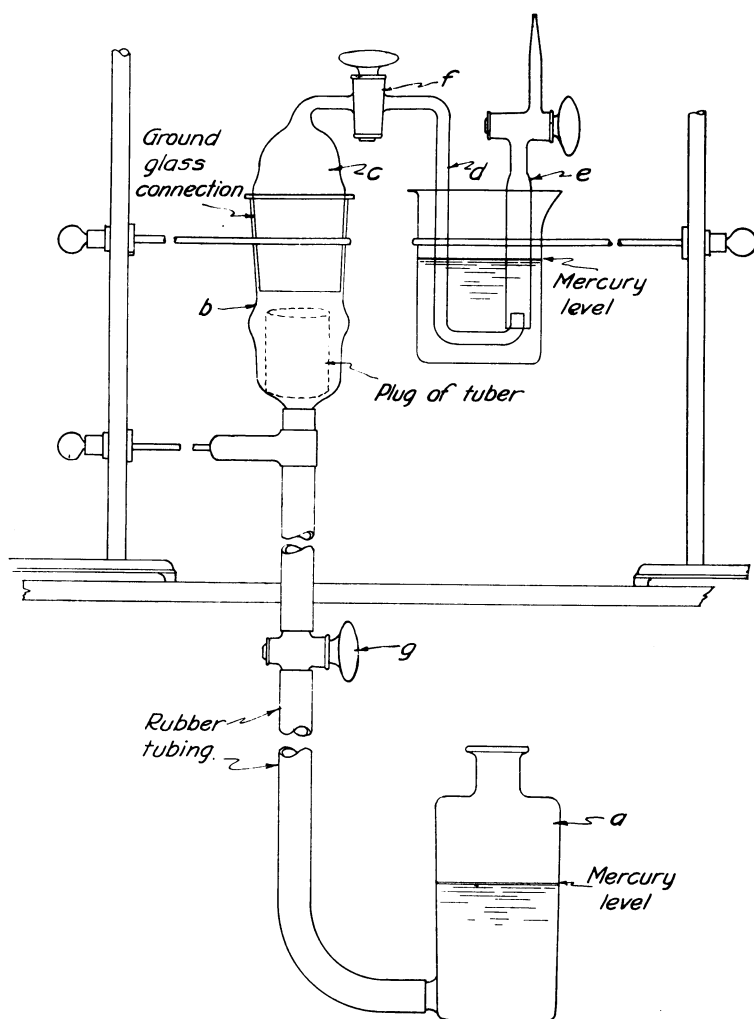


Fig. 3. Apparatus used for extracting gas from tubers. Cylinder (b) is partially filled with mercury by raising levelling bottle (a). The plug of tuber is then pushed from the cork borer under the mercury in cylinder (b), and stopper (e) is inserted and made tight. With stopcocks (f) and (g) open, the cylinder (e) and tube (d) are filled with mercury. Stopcock (f) is then closed and levelling bottle (a) is lowered, creating a Torricellian vacuum in tube (d) and part of cylinder (b). After two minutes, levelling bottle (a) is raised, stopcock (f) is opened, and the gas extracted from the tuber plug is collected and measured over mercury in burette (e).

the rates both of loss of carbon dioxide and absorption of oxygen. Data regarding length of rest period, composition of interior gas, and rates of gaseous exchange of the two varieties are shown in tables 2 to 5.

In general, the untreated dry lots gradually decrease during storage in rate of carbon dioxide given off and oxygen absorbed; the untreated moist lots increase slightly in rate of loss of carbon dioxide, but remain about the same or drop slightly in absorption of oxygen for a week or more, and then usually rise somewhat after the appear-

TABLE 2
RELATION OF RESPIRATION RATES TO COMPOSITION OF INTERIOR GAS OF WHITE ROSE TUBERS TREATED JANUARY 30-31. STORED JANUARY 30

Treatment*	Jan. 31	Feb. 4	Feb. 7	Feb. 12	Feb. 19					
	Milligrams carbon dioxide per kgm. hour respired									
Untreated dry.....	8.1	6.2	4.8	5.9	5.4†					
Untreated moist.....		10.7	9.9	10.3†	10.5					
Treated dry.....		14.8	13.7	9.2†	8.3					
	Milligrams oxygen per kgm. hour absorbed									
Untreated dry.....	8.4	6.2	6.7	5.5	5.2†					
Untreated moist.....		8.5	9.6	7.5†	8.9					
Treated dry.....		12.2	12.0	7.6†	7.6					
	Feb. 2	Feb. 4	Feb. 8	Feb. 13	Feb. 19					
	Composition of interior gas, per cent									
	CO ₂	O ₂	CO ₂	O ₂	CO ₂	O ₂	CO ₂	O ₂	CO ₂	O ₂
Untreated dry.....	10.4	14.1	10.4	13.7	8.5	14.4	15.2	13.9	14.0	15.6
Untreated moist.....			22.4	11.7	15.0	12.0	17.9	12.2	18.8	10.2
Treated dry.....			13.3	12.5	10.8	14.5	15.5	13.6	10.3	16.6
	Sum of percentages of carbon dioxide and oxygen in interior gas and CO ₂ /O ₂ ratio									
	Ratio	Sum	Ratio	Sum	Ratio	Sum	Ratio	Sum	Ratio	Sum
Untreated dry.....	0.74	24.5	0.76	24.1	0.59	22.9	1.10	29.1	0.90	29.6
Untreated moist.....			1.92	34.1	1.25	27.0	1.47	30.1	1.85	29.0
Treated dry.....			1.06	25.8	0.75	25.3	1.14	29.1	0.62	26.9

* These names are shortened designations for chemically untreated, dry-stored; chemically untreated, moist-stored; and ethylene-chlorhydrin-treated, dry-stored.

† All tubers sprouted. Sprouts removed on this date.

ance of sprouts. Treated dry lots increase rapidly within three or four days after treatment and then gradually decline in rates of loss of carbon dioxide and of absorption of oxygen. Several days more are required to show the full effects of moist storage upon rate of respiration than to show the effects of ethylene chlorhydrin treatment. With those treatments that abbreviate the rest period there is a striking increase in the rate of absorption of oxygen as well as an increase in the rate of loss of carbon dioxide.

Effects on Composition of Interior Gas.—The data of tables 2 and 3 show that the general tendency in all treatments of both varieties is for the carbon dioxide percentage of the interior gas to increase during storage, with the exception of a period just before or at the time

TABLE 3

RELATION OF RESPIRATION RATES TO COMPOSITION OF INTERIOR GAS OF IRISH COBBLER TUBERS TREATED JANUARY 30–31. STORED JANUARY 30

Treatment*	Jan. 31	Feb. 4	Feb. 7	Feb. 12	Feb. 19					
	Milligrams carbon dioxide per kgm. hour respired									
Untreated dry.....	8.5	7.3	5.5	4.7	5.8†					
Untreated moist.....		7.3	10.1	8.7†	7.9					
Treated dry.....		12.4	9.0	8.6†	7.7					
	Milligrams oxygen per kgm. hour absorbed									
Untreated dry.....	9.5	7.2	6.3	4.3	5.8†					
Untreated moist.....		6.7	8.9	6.3†	6.9					
Treated dry.....		10.9	9.4	7.0†	7.2					
	Feb. 2	Feb. 4	Feb. 7	Feb. 12	Feb. 19					
	Composition of interior gas, per cent									
	CO ₂	O ₂	CO ₂	O ₂	CO ₂	O ₂	CO ₂	O ₂	CO ₂	O ₂
Untreated dry.....	12.1	15.6	15.0	13.2	8.0	14.7	13.1	14.5	16.7	13.1
Untreated moist.....			14.5	12.7	15.8	11.0	20.6	11.0	21.8	10.6
Treated dry.....			15.0	15.1	11.4	14.0	15.5	13.6	17.0	14.4
	Sum of percentages of carbon dioxide and oxygen in interior gas and CO ₂ /O ₂ ratio									
	Ratio	Sum	Ratio	Sum	Ratio	Sum	Ratio	Sum	Ratio	Sum
Untreated dry.....	0.76	22.7	1.14	28.2	0.55	22.7	0.91	27.6	1.28	29.8
Untreated moist.....			1.14	27.2	1.44	26.8	1.87	31.6	2.06	32.4
Treated dry.....			0.99	30.1	0.81	25.4	1.14	29.1	1.17	31.6

* These names are shortened designations for chemically untreated, dry-stored; chemically untreated, moist-stored; and ethylene-chlorhydrin-treated, dry-stored.

† All tubers sprouted. Sprouts removed on this date.

the sprouts appear, when a decrease occurs, followed by an increase. No constant differences are shown between the two varieties in carbon dioxide or oxygen percentages.

In an attempt to find whether any of the treatments described above had affected the permeability of the tubers to carbon dioxide, every reading of carbon dioxide respired and per cent of carbon dioxide in interior gas (see tables 2 and 3) of each of the treat-

TABLE 4

RELATIVE PERMEABILITY OF TREATED AND UNTREATED WHITE ROSE TUBERS TO CARBON DIOXIDE, FOUND BY COMPARISON OF EXPERIMENTALLY DETERMINED AND CALCULATED VALUES* OF PERCENTAGE OF CARBON DIOXIDE IN INTERIOR GAS OF TUBERS

Tubers treated and stored January 30-31

Treatments compared†	Per cent carbon dioxide in interior gas of the latter member of each comparison							
	Feb. 4		Feb. 7		Feb. 12		Feb. 19	
	Det.	Calc.	Det.	Calc.	Det.	Calc.	Det.	Calc.
Untreated dry <i>vs.</i> untreated moist.....	22.4	18.0	15.0	17.5	17.9	26.5	18.8	27.3
Untreated dry <i>vs.</i> treated dry.....	13.3	24.8	10.8	24.3	15.5	23.7	10.3	21.5
Untreated moist <i>vs.</i> treated dry.....	13.3	31.0	10.8	20.8	15.5	16.0	10.3	14.9

* Example.—Untreated dry compared with untreated moist expressed in the form of a proportion: (1) the rate of loss of carbon dioxide from untreated dry stored is to (2) the percentage of carbon dioxide in the interior gas of untreated dry stored as (3) the rate of loss of carbon dioxide from untreated moist stored is to (4) the percentage of carbon dioxide in the interior gas of untreated moist stored lots. By analyses these are found to be (1) (2) (3) (4)
6.2 : 10.4 : : 10.7 : 22.4. This is not a true proportion, however, as the

fourth term is too large. By calculation, the fourth term has a value of 18.0. If this calculated figure is larger than the figure determined by analysis, the tubers of the second member of the compared treatments, in the table above, are more permeable than the first; if smaller than the determined figure, those of the second member are less permeable than the first.

† These names are shortened designations for chemically-untreated, dry-stored; chemically-untreated, moist-stored; and ethylene-chlorhydrin-treated, dry-stored.

TABLE 5

RELATIVE PERMEABILITY OF UNTREATED AND TREATED IRISH COBBLER TUBERS TO CARBON DIOXIDE, FOUND BY COMPARISON OF EXPERIMENTALLY DETERMINED AND CALCULATED VALUES* OF PERCENTAGE OF CARBON DIOXIDE IN INTERIOR GAS OF TUBERS

Tubers treated and stored January 30-31

Treatments† compared	Per cent carbon dioxide in interior gas of the latter member of each comparison							
	Feb. 4		Feb. 7		Feb. 12		Feb. 19	
	Det.	Calc.	Det.	Calc.	Det.	Calc.	Det.	Calc.
Untreated dry <i>vs.</i> untreated moist.....	14.5	15.0	15.8	14.7	20.6	24.2	21.8	22.8
Untreated dry <i>vs.</i> treated dry.....	15.0	25.5	11.4	13.1	15.5	24.0	17.0	22.2
Untreated moist <i>vs.</i> treated dry.....	15.0	24.6	11.4	14.1	15.5	20.4	17.0	21.2

* The calculated values were obtained by ratios of rate of carbon dioxide loss and percentage of carbon dioxide in the interior gas of the compared treatments. A greater calculated than determined value indicates a probable greater permeability of the second member of the comparison. See footnote to table 4.

† These names are shortened designations for chemically untreated, dry-stored; chemically untreated, moist-stored; and ethylene-chlorhydrin-treated, dry-stored.

ments was compared with the readings of all the others. These experimentally determined and calculated values are presented and compared in tables 4 and 5. In all lots the weights, number, size, and shape of the tubers, and therefore the surface areas, were approximately equal. A calculated value lower than the experimentally determined value apparently indicates that the tubers of the lot of the second member (see tables 4 and 5) of each pair of compared members are less permeable to the gas than the tubers of the lot of the first member with which they are compared. The data of table 4 on White Rose indicate that for the first few days after storage, the tubers of the untreated moist lots are less permeable to carbon dioxide than the untreated dry lots, but thereafter surpass the untreated dry lots and become increasingly permeable during the storage period. Just after treatment, the treated dry lots become much more permeable than either the untreated dry or untreated moist lots; but gradually, during storage, they become less so. The data of table 5 on Irish Cobbler follow the same trend as those on White Rose, although in general they show less activity than the White Rose. Data on loss of carbon dioxide and absorption of oxygen in table 3 show very small differences early in the storage period between untreated dry and untreated moist lots. The comparisons of these two sets of data in tables 4 and 5 show also a less striking increase in permeability to carbon dioxide of the untreated moist over the untreated dry Irish Cobbler tubers than in the case of the White Rose tubers.

EXPERIMENTS ON WHITE ROSE TUBERS, TREATED AND UNTREATED, DRY AND MOIST-STORED

Experimental Procedure.—White Rose tubers, dug on November 10, were held at 8° to 10° C until February 8, 9, 10, and 11, when they were treated with ethylene chlorhydrin, stored at 25° C, and divided into the following four lots: (1) untreated dry, (2) untreated moist, (3) treated dry, and (4) treated moist. At four to seven-day intervals the tubers were analyzed for rate of loss of carbon dioxide, absorption of oxygen, and composition of interior gas. These determinations were replicated six times, with a total of 30 tubers for each determination when finally calculated.

Effects on Rate of Respiration.—The rates of loss of carbon dioxide and absorption of oxygen throughout the storage period (table 6) are typical of all the lots which have been described above in the series comparing White Rose and Irish Cobbler tubers untreated and treated with ethylene chlorhydrin when dry and when moist-

stored. The initial rate of loss of carbon dioxide and absorption of oxygen of the untreated moist lots is usually higher than that of the untreated dry lots; these rates, however, gradually increase in the moist lots but decrease in the dry lots. The effects of moist storage

TABLE 6

RELATION OF RESPIRATION RATES TO COMPOSITION OF INTERIOR GAS OF WHITE ROSE TUBERS STORED AT 25° C, AVERAGE OF 6 REPLICATES

Treatment*	Feb. 9-10	Feb. 13-14	Feb. 17-18	Feb. 22-23	Feb. 27-28	March 6-7						
	Milligrams carbon dioxide per kgm. hour respired											
Untreated dry.....	7.2	7.3	5.4	4.8	5.0†	4.2						
Untreated moist.....		8.6	8.9	10.7†	14.2	14.1						
Treated dry.....		9.0	6.6	5.8†	6.0	5.7						
Treated moist.....		13.1	11.5	12.7†	14.4	12.2						
	Milligrams oxygen per kgm. hour absorbed											
Untreated dry.....	7.5	7.6	8.4	5.1	4.1†	4.6						
Untreated moist.....		7.7	8.1	8.4†	10.2	11.2						
Treated dry.....		9.1	7.1	6.9†	5.5	5.6						
Treated moist.....		10.1	9.6	8.5†	10.4	9.5						
	Composition of interior gas in per cent											
	CO ₂	O ₂	CO ₂	O ₂	CO ₂	O ₂	CO ₂	O ₂	CO ₂	O ₂	CO ₂	O ₂
Untreated dry.....	2.5	18.8	6.4	16.2	7.5	15.7	6.0	15.1	8.8	14.5	12.1	15.3
Untreated moist.....			13.1	11.9	14.8	11.1	13.1	11.7	17.6	11.5	24.3	10.9
Treated dry.....			11.3	12.8	11.7	14.1	12.1	13.3	13.9	14.7	16.8	13.7
Treated moist.....			12.6	13.9	13.0	14.0	12.0	13.6	17.3	11.3	25.5	12.1
	Sum of percentage of carbon dioxide and oxygen in interior gas and CO ₂ /O ₂ ratio											
	Sum	Ratio	Sum	Ratio	Sum	Ratio	Sum	Ratio	Sum	Ratio	Sum	Ratio
Untreated dry.....	21.3	0.13	22.6	0.39	23.2	0.48	21.1	0.40	23.4	0.60	27.4	0.79
Untreated moist.....			25.0	1.10	25.9	1.34	24.8	1.12	29.1	1.53	35.2	2.33
Treated dry.....			24.1	0.89	25.8	0.83	25.4	0.91	28.6	0.95	30.5	1.23
Treated moist.....			26.5	0.91	27.0	0.93	25.6	0.88	27.8	1.53	37.6	2.11

* These names are shortened designations for chemically untreated, dry-stored; chemically untreated, moist-stored; ethylene-chlorhydrin-treated, dry-stored; and ethylene-chlorhydrin-treated, moist-stored.

† All tubers sprouted. Sprouts removed on this date.

upon the rate of loss of carbon dioxide and absorption of oxygen are much more delayed than in the treatment with ethylene chlorhydrin. In all treatments that shorten the rest period more oxygen is absorbed than in the untreated dry lots.

Effects on Composition of Interior Gas.—With all treatments, the percentage of carbon dioxide gradually increases during storage, and then decreases about the time of sprout appearance, after which it

risers to a higher percentage than before the decline. Generally the percentage of carbon dioxide is higher in moist than in dry lots; higher in untreated moist than in treated dry lots; usually higher in untreated moist than treated moist lots in the early storage period, but somewhat lower than the latter after several weeks of storage. The percentage of oxygen is lowest as a rule in the untreated moist lots, although in general less carbon dioxide and more oxygen occur in the untreated moist than in the untreated dry lots in proportion to the amounts of carbon dioxide given off and oxygen absorbed by these lots.

TABLE 7

RELATIVE PERMEABILITY OF UNTREATED AND TREATED WHITE ROSE TUBERS TO CARBON DIOXIDE, FOUND BY COMPARISON OF EXPERIMENTALLY DETERMINED AND CALCULATED VALUES* OF PERCENTAGE OF CARBON DIOXIDE IN INTERIOR GAS OF TUBERS

Treated and stored at 25° C, February 8-11, averages of 6 replicates

Treatments† compared	Per cent carbon dioxide in interior gas of the latter member of each comparison									
	Feb. 13-14		Feb. 17-18		Feb. 22-23		Feb. 27-28		March 6-7	
	Det.	Calc.	Det.	Calc.	Det.	Calc.	Det.	Calc.	Det.	Calc.
Untreated dry <i>vs.</i> untreated moist.....	13.1	7.5	14.8	12.4	13.1	13.4	17.6	25.0	24.3	40.6
Untreated dry <i>vs.</i> treated dry.....	11.3	7.9	11.7	9.2	12.1	7.3	13.9	10.6	16.8	16.4
Untreated dry <i>vs.</i> treated moist.....	12.6	11.5	13.0	16.0	12.0	15.9	17.3	25.3	25.5	35.2
Untreated moist <i>vs.</i> treated dry.....	11.3	13.7	11.7	11.0	12.1	7.1	13.9	7.4	16.8	9.8
Untreated moist <i>vs.</i> treated moist.....	12.6	20.0	13.0	19.2	12.0	15.6	17.3	17.9	25.5	21.0
Treated dry <i>vs.</i> treated moist.....	12.6	16.5	13.0	20.4	12.0	26.5	17.3	33.4	25.5	36.0

* The calculated values were obtained by ratios of rate of carbon dioxide loss and percentage of carbon dioxide in the interior gas of the compared treatments. A greater calculated than determined value indicates a probable greater permeability of the second member of the comparison. See footnote to table 4.

† These names are shortened designations for chemically untreated, dry-stored; chemically untreated, moist-stored; ethylene-chlorhydrin-treated, dry-stored; and ethylene-chlorhydrin-treated, moist-treated.

In general the same relations exist between the ratios of the carbon dioxide to oxygen in the different lots as between the percentages of carbon dioxide in the interior gas of the tubers. The oxygen percentages of the tubers of the treated and moist lots do not decrease in so great amounts as the carbon dioxide increases in these same treatments. These relations are shown by the sums of carbon dioxide plus oxygen in the interior gas, which are usually of greater magnitude in the treated lots than in the untreated and also greater in the moist than in the dry lots.

In table 7 are presented the compared calculated and experimentally determined values which indicate the relative permeability

of the tubers in the various lots to carbon dioxide. These data indicate (1) that early in the storage period the untreated dry lots are more permeable than the untreated moist lots, but that after eight or nine days in storage the latter are more permeable; (2) that untreated dry lots are more permeable than treated dry lots, for the first few weeks of storage, but that after nearly four weeks the two are approximately equal; (3) that treated moist lots, with the exception of the first determination four days after treatment, are more permeable than the untreated dry lots and increase rapidly over the latter; (4) that untreated moist lots are more permeable than the treated dry lots, and become increasingly more so during storage; (5) that treated moist lots are more permeable than the untreated moist lots early after treatment and for several weeks thereafter, but gradually become less so until about four weeks after treatment, when the treated moist lots are less permeable than the untreated moist lots; and (6) that treated moist lots are consistently more permeable than the treated dry lots.

EXPERIMENTS ON DRY AND MOIST TUBERS IN JARS CONTAINING AIR AND A HIGH PERCENTAGE OF OXYGEN WITH AND WITHOUT THE ACCUMULATION OF CARBON DIOXIDE

Experimental Procedure.—White Rose tubers were dug on November 10. From November 10 to February 12 the tubers of the first test were stored at 8° to 10° C. On February 12 they were placed in storage at 25° C, and on February 20 they were divided into lots of four tubers each, weighing 677 grams per lot, which were sealed in one-gallon glass jars for a period of 48 hours: (1) air, KOH, dry; (2) air, no KOH, dry; (3) O₂, KOH, dry; (4) O₂, no KOH, dry; (5) O₂, KOH, moist; (6) O₂, no KOH, moist; (7) air, KOH, moist; (8) air, no KOH, moist. These abbreviations have the following meanings:

‘Air’: the gas surrounding the tubers was air, analyzing 20.6 per cent oxygen and 0.0 per cent carbon dioxide.

‘KOH’: 100 cc of a 50 per cent solution of potassium hydroxide was placed in the bottom of the jar.

‘Dry’: no moistening or drying agent was used.

‘No KOH’: no potassium hydroxide solution was used.

‘O₂’: the gas surrounding the tubers contained 60 per cent oxygen.

'Moist': the tubers were packed in moist sphagnum moss.

Another lot of tubers, not placed in jars, was used for analysis of interior gas as a check on those in the jars.

Four other experiments were run also, beginning February 14 and March 4, 6, and 8. In experiment 2, lots 6 and 8 were omitted.

Check jars without tubers but with moist moss were used to determine the amounts of carbon dioxide given off and of oxygen absorbed by the moss and water. The final data given in the tables are corrected for these figures. After 48 hours the amounts of carbon dioxide given off, the oxygen absorbed, and the composition of gas of the interior of the tubers were determined.

TABLE 8

RELATION OF RESPIRATION RATES TO COMPOSITION OF INTERIOR GAS OF WHITE ROSE TUBERS, FEBRUARY 14

Six tubers in each jar; weight 478-536 grams; stored January 24 at 25° C

Treatments*	Respiration rate		Composition of interior gas of tuber, per cent			Total CO ₂ plus O ₂	Composition of gas in jars when opened per cent		CO ₂ /O ₂ ratio of gas	
	Mgms. CO ₂ per kgm. hour	Mgms. O ₂ per kgm. hour	CO ₂	O ₂	N ₂		CO ₂	O ₂	From interior of tubers	In jar when op'n'd
Untreated (check).....			5.0	17.0	78.0	22.0			0.29	
Air, KOH, dry.....		6.0	5.5	16.7	77.8	22.2	0.0	16.8	0.33	
Air, no KOH, dry.....	4.9	5.3	13.6	13.9	72.5	27.5	2.2	17.8	0.98	0.12
O ₂ , KOH, dry.....		6.4	7.9	24.6	67.5	32.5	0.0	56.3	0.32	
O ₂ , no KOH, dry.....	5.4	5.5	10.0	30.3	59.7	40.3	1.9	57.1	0.33	0.033
O ₂ , KOH, moist.....		29.7	17.6	17.9	64.5	35.5	0.0	36.8	0.98	
Air, KOH, moist.....		25.8	6.1	8.2	85.7	14.3	0.0	0.3	0.75	

* See text for explanation of treatments.

TABLE 9

RELATION OF RESPIRATION RATES TO COMPOSITION OF INTERIOR GAS OF WHITE ROSE TUBERS, FEBRUARY 20

Four tubers in each jar; weight 677 grams; stored February 12 at 25° C

Treatments*	Respiration rate		Composition of interior gas of tuber, per cent			Total CO ₂ plus O ₂	Composition of gas in jars when opened per cent		CO ₂ /O ₂ ratio of gas	
	Mgms. CO ₂ per kgm. hour	Mgms. O ₂ per kgm. hour	CO ₂	O ₂	N ₂		CO ₂	O ₂	From interior of tubers	In jar when op'n'd
Untreated (check).....			11.0	15.2	73.8	26.2			0.72
Air, KOH, dry.....		5.4	11.2	14.6	74.2	25.8	0.0	16.2	0.77
Air, no KOH, dry.....	4.8	5.3	20.3	13.0	66.7	33.3	2.8	16.4	1.56	0.17
O ₂ , KOH, dry.....		6.9	12.1	29.1	58.8	41.2	0.0	54.5	0.42
O ₂ , no KOH, dry.....	5.2	6.3	23.9	31.5	44.6	55.4	3.0	55.0	0.76	0.055
O ₂ , KOH, moist.....		13.9	27.4	22.1	50.5	49.5	0.0	42.4	1.24
O ₂ , no KOH, moist.....	5.3	10.9	27.6	24.2	48.2	51.8	4.2	51.1	1.14	0.082
Air, KOH, moist.....		12.2	17.9	10.6	71.5	28.5	0.0	5.0	1.69
Air, no KOH, moist.....	4.9	9.9	30.6	7.0	62.4	37.6	3.8	9.5	4.37	0.40

* See text for explanation of treatments.

TABLE 10

RELATION OF RESPIRATION RATES TO COMPOSITION OF INTERIOR GAS OF WHITE ROSE TUBERS; MARCH 4

Five tubers in each jar; weight 630 grams; stored February 22 at 25° C

Treatments*	Respiration rate		Composition of interior gas of tuber, per cent			Total CO ₂ plus O ₂	Composition of gas in jars when opened per cent		CO ₂ /O ₂ ratio of gas	
	Mgms. CO ₂ per kgm. hour	Mgms. O ₂ per kgm. hour					CO ₂	O ₂	N ₂	CO ₂
Untreated (check).....			10.1	16.0	73.9	26.1			0.63	
Air, KOH, dry.....		5.5	10.6	15.2	74.2	25.8	0.0	15.9	0.70	
Air, no KOH, dry.....	4.9	5.3	19.4	13.7	66.9	33.1	2.4	16.2	1.42	0.150
O ₂ , KOH, dry.....		6.9	11.2	31.1	57.7	42.3	0.0	52.3	0.36	
O ₂ , no KOH, dry.....	5.4	6.2	22.8	32.6	44.6	55.4	2.7	53.4	0.70	0.051
O ₂ , KOH, moist.....		14.8	26.1	24.2	49.7	50.3	0.0	41.2	1.08	
O ₂ , no KOH, moist.....	5.5	12.2	27.0	26.8	46.2	53.8	3.8	50.3	1.01	0.076
Air, KOH, moist.....		13.6	16.0	11.8	72.2	27.8	0.0	5.1	1.36	
Air, no KOH, moist.....	5.0	10.3	28.1	8.8	63.1	36.9	3.5	9.2	3.20	0.380

* See text for explanation of treatments.

TABLE 11

RELATION OF RESPIRATION RATES TO COMPOSITION OF INTERIOR GAS OF WHITE ROSE TUBERS; MARCH 6

Five tubers in each jar; weight 613 grams; stored March 3 at 25° C

Treatments*	Respiration rate		Composition of interior gas of tuber, per cent			Total CO ₂ plus O ₂	Composition of gas in jars when opened per cent		CO ₂ /O ₂ ratio of gas	
	Mgms. CO ₂ per kgm. hour	Mgms. O ₂ per kgm. hour					CO ₂	O ₂	N ₂	CO ₂
Untreated (check).....			9.9	16.3	73.8	26.2			0.61	
Air, KOH, dry.....		5.6	10.3	15.8	73.9	26.1	0.0	16.0	0.65	
Air, no KOH, dry.....	5.0	5.4	18.8	13.6	67.6	32.4	2.3	16.3	1.39	0.14
O ₂ , KOH, dry.....		6.9	11.1	32.0	56.9	43.1	0.0	53.2	0.35	
O ₂ , no KOH, dry.....	5.4	6.3	22.2	33.2	44.6	55.4	2.5	53.9	0.67	0.047
O ₂ , KOH, moist.....		15.1	24.5	25.3	50.2	49.8	0.0	42.1	0.97	
O ₂ , no KOH, moist.....	5.8	12.6	26.0	27.1	46.9	53.1	3.7	50.9	0.96	0.073
Air, KOH, moist.....		14.1	16.1	12.3	71.7	28.3	0.0	6.2	1.31	
Air, no KOH, moist.....	5.1	10.1	27.6	9.7	62.7	37.3	3.3	9.1	2.85	0.370

* See text for explanation of treatments.

Effects on Rate of Respiration.—The data presented in tables 8 to 12 indicate that the presence of potassium hydroxide solution in the respiration jars slightly increases the rate of oxygen absorption by the tubers. This is very strikingly shown by those lots surrounded by gas containing 60 per cent oxygen; they absorb more of this gas and give off slightly more carbon dioxide than those in air, which are otherwise receiving the same treatments. Moist tubers absorb oxygen and respire carbon dioxide more rapidly than the dry tubers.

Effect on Composition of Interior Gas.—The presence of potassium hydroxide in the jars lowers the percentage of carbon dioxide in the interior gas. The presence of the potassium hydroxide solution increases the percentage of oxygen found in the tubers surrounded by air; but the presence of the potassium hydroxide solution decreases the percentage of this gas found in the tubers surrounded by 60 per cent oxygen.

The percentage of oxygen in tubers surrounded by an atmosphere with a large proportion of this gas is higher, and the percentage of

TABLE 12

RELATION OF RESPIRATION RATES TO COMPOSITION OF INTERIOR GAS OF WHITE ROSE TUBERS; MARCH 8

Five tubers in each jar; weight 622 grams; stored March 3 at 25° C.

Treatments*	Respiration rate		Composition of interior gas of tuber, per cent			Total CO ₂ plus O ₂	Composition of gas in jars when opened per cent		CO ₂ /O ₂ ratio of gas	
	Mgms. CO ₂ per kgm. hour	Mgms. O ₂ per kgm. hour	CO ₂	O ₂	N ₂		CO ₂	O ₂	From interior of tubers	In jar when op'n'd
Untreated (check).....			10.2	16.2	73.6	26.4			0.63	
Air, KOH, dry.....		5.7	10.5	15.5	74.0	26.0	0.0	16.2	0.68	
Air, no KOH, dry.....	5.2	5.4	19.0	13.4	67.6	32.4	2.4	16.3	1.42	0.15
O ₂ , KOH, dry.....		6.8	11.6	31.8	56.6	43.4	0.0	51.7	0.37	
O ₂ , no KOH, dry.....	5.6	6.2	22.4	33.3	44.3	55.7	2.6	52.3	0.67	0.05
O ₂ , KOH, moist.....		15.4	24.2	25.2	50.6	49.4	0.0	40.1	0.96	
O ₂ , no KOH, moist.....	5.9	12.8	26.1	27.4	46.5	53.5	3.9	49.3	0.95	0.079
Air, KOH, moist.....		14.5	16.4	12.6	71.0	29.0	0.0	5.3	1.30	
Air, no KOH, moist.....	5.2	10.2	27.7	9.9	62.4	37.6	3.6	9.5	2.80	0.38

* See text for explanation of treatments.

carbon dioxide, with the exception of one treatment, is also higher, than in tubers in air otherwise receiving the same treatment.

The percentage of carbon dioxide is higher and of oxygen lower in moist than in dry tubers; but the increase of rates of carbon dioxide loss and oxygen absorption is larger in the moist tubers than the increased percentage of carbon dioxide and decreased percentage of oxygen found in them, as compared with the dry tubers.

Only one treatment, 'air, KOH, moist,' had a higher percentage of oxygen in the tubers than in the surrounding atmosphere in the jar when the jar was opened. The small tubers with more surface exposed per unit of volume absorb oxygen at a higher rate than the large tubers.

PERMEABILITY OF PERIDERM TO GAS

Experimental Procedure.—Small, sound tubers, selected on the date of harvest, were stored at 8° to 10° C at intervals beginning November 10 with White Rose and December 1 with Irish Cobbler. These lots, in duplicate, of eight tubers each, approximately alike in size and shape, were selected for the same weight in each lot. Lot 1 was chemically untreated, stored dry; lot 2 was chemically untreated, stored moist; and lot 3 was treated with ethylene chlorhydrin and stored dry. All were stored at 25° C on the date of the first determination. At four to seven-day intervals, gas was extracted through the uninjured periderm for two minutes into a Torricellian vacuum with the instrument described and shown in figure 3. These gases were collected, and the amounts extracted from each lot were measured. Lots of White Rose were started on November 10, 22, and 27, on December 1 and 5, and on January 5, 9, 14, and 22. Lots of Irish Cobbler were started on December 1, 5, and 11, and on January 8. In order not to present so many figures, the tables give only the data on White Rose started on November 10, December 1, and January 14, and on Irish Cobbler on December 1 and January 8.

Small tubers similar to those used in the above experiments were studied in an effort to find what change, if any, in amounts and composition of gas extracted would result from the removal of a thin layer of periderm. Two lots of tubers of equal numbers, size, and total weight were selected, and the gas was drawn out, measured, and analyzed. One lot was then peeled, and the gases were immediately extracted again, measured, and analyzed. These lots were run in duplicate.

Effects on Amounts of Gas Extracted.—The data of these experiments are presented in tables 13 to 17. The amount of gas withdrawn from the White Rose tubers gradually diminishes with each lot as the interval between harvest and first extraction of gas increases, from November 10 to January 22. The same is true of Irish Cobbler tubers with gas withdrawn at intervals from December 1 to January 8. Because of careful selection of tubers in each lot for equality of size, shape, and weight, the differences in amount of gas withdrawn from the different lots at the first extraction before treatment were never more than 0.1 cc. Extractions made soon after harvest show that the amounts from the untreated dry lots slightly increased during storage at four or five-day intervals, but the lots started later after digging showed a steady decrease in the amount of gas extracted from the

untreated dry lots during the period of storage. Within each particular lot during the period of storage, and also in the initial extraction of each succeeding experiment, the untreated moist and treated dry lots give off more gas into the partial vacuum than the untreated

TABLE 13

AMOUNT OF GAS EXTRACTED FROM WHOLE WHITE ROSE TUBERS; TREATED AND STORED NOVEMBER 10

Eight tubers; 175 grams; average of duplicate samples

Treatment	Nov. 10	Nov. 15	Nov. 20	Nov. 24
	Cubic centimeters of gas extracted			
Chemically untreated, dry-stored.....	5.3	5.4	5.6	5.7
Chemically untreated, moist-stored.....	5.2	6.2	6.8	7.8
Ethylene-chlorhydrin-treated, dry-stored.....	5.2	6.2	6.7	7.3
Per cent increase over chemically untreated, dry-stored				
Chemically untreated, moist-stored.....		14.8	21.4	36.9
Ethylene-chlorhydrin-treated, dry-stored.....		14.8	19.6	28.0

TABLE 14

AMOUNT OF GAS EXTRACTED FROM WHOLE WHITE ROSE TUBERS; TREATED AND STORED DECEMBER 1

Eight tubers; 180 grams; average of duplicate samples

Treatment	Dec. 1.	Dec. 5	Dec. 10	Dec. 15
	Cubic centimeters of gas extracted			
Chemically untreated, dry-stored.....	4.8	4.6	4.5	4.3
Chemically untreated, moist-stored.....	4.7	5.1	5.2	5.3
Ethylene-chlorhydrin-treated, dry-stored.....	4.8	5.0	5.0	5.0
Per cent increase over chemically untreated, dry-stored				
Chemically untreated, moist-stored.....		10.8	15.5	23.2
Ethylene-chlorhydrin-treated, dry-stored.....		8.7	11.1	16.2

dry lots. The differences, however, become less as the end of the rest period is approached, until the gain of the treated and moist-stored lots over the untreated dry lots is negligible. During the early stages of the rest period, soon after harvest, more gas is extracted from the untreated moist-stored lots than from the treated, dry-stored; but later in the rest period, the treated dry-stored lots often give larger amounts of gas than the untreated moist-stored lots. Interestingly enough, those treatments that shorten the rest period

TABLE 15

AMOUNT OF GAS EXTRACTED FROM WHOLE WHITE ROSE TUBERS; TREATED AND STORED JANUARY 14

Eight tubers; 172 grams; average of duplicate samples

Treatment	Jan. 14	Jan. 19	Jan. 24	Jan. 28
	Cubic centimeters of gas extracted			
Chemically untreated, dry-stored.....	4.5	4.1	3.9	3.6
Chemically untreated, moist-stored.....	4.4	4.1	4.2	3.9
Ethylene-chlorhydrin-treated, dry-stored.....	4.5	4.2	4.1	3.95
	Per cent increase over chemically untreated, dry-stored			
Chemically untreated, moist-stored.....		0.0	7.7	8.3
Ethylene-chlorhydrin-treated, dry-stored.....		2.4	5.1	9.7

TABLE 16

AMOUNT OF GAS EXTRACTED FROM WHOLE IRISH COBBLER TUBERS; TREATED AND STORED DECEMBER 1

Eight tubers; 180 grams; average of duplicate samples

Treatment	Dec. 1	Dec. 6	Dec. 11	Dec. 16
	Cubic centimeters of gas extracted			
Chemically untreated, dry-stored.....	5.0	4.7	4.3	4.2
Chemically untreated, moist-stored.....	5.0	5.2	5.5	5.7
Ethylene-chlorhydrin-treated, dry-stored.....	4.9	5.3	5.5	5.6
	Per cent increase over chemically untreated, dry-stored			
Chemically untreated, moist-stored.....		10.6	27.9	35.7
Ethylene-chlorhydrin-treated, dry-stored.....		12.8	27.9	33.3

TABLE 17

AMOUNT OF GAS EXTRACTED FROM WHOLE IRISH COBBLER TUBERS; TREATED AND STORED JANUARY 8

Eight tubers; 170 grams; average of duplicate samples

Treatment	Jan. 8	Jan. 12	Jan. 17	Jan. 31
	Cubic centimeters of gas extracted			
Chemically untreated, dry-stored.....	4.5	4.0	4.0	3.8
Chemically untreated, moist-stored.....	4.4	4.1	4.4	4.3
Ethylene-chlorhydrin-treated, dry-stored.....	4.4	4.4	4.5	4.3
	Per cent increase over chemically untreated, dry-stored			
Chemically untreated, moist-stored.....		2.5	10.0	13.1
Ethylene-chlorhydrin-treated, dry-stored.....		10.0	12.5	13.1

also increase the permeability of the skin to gas; and the time during the rest period when the treatments are made influences both the length of the rest period and the amount of gas extracted.

Data comparing the amounts and composition of gas withdrawn from peeled and unpeeled tubers are presented in tables 18 to 21. Removing the periderm and a thin layer of cortex increases the amount of gas extracted. As these increases are not of very great magnitude, the relative permeability of the tissue in the interior of the tubers is probably rather low and the periderm is most likely

TABLE 18
EFFECT OF PEELING ON AMOUNT AND COMPOSITION OF GAS EXTRACTED FROM
WHITE ROSE TUBERS, FEBRUARY 21

Twelve tubers in each lot; weight 265 grams; stored at 25° C; average
of duplicate samples

Treatment		Gas extracted, cc	Composition of interior gas, per cent		Total CO ₂ plus O ₂	Per cent N ₂ , by difference
			CO ₂	O ₂		
Lot 1	Before peeling.....	6.2	6.7	18.2	24.9	75.1
	Immediately after peeling.....	6.5	10.9	17.3	28.2	71.2
	Three days after peeling.....	5.75	8.8	18.7	26.9	73.1
Lot 2	Not peeled.....	5.95	5.8	19.1	24.9	75.1
	Not peeled (immediately after first extraction)....	5.85	3.9	19.4	23.3	76.7
	Not peeled, three days later.....	5.65	6.0	18.0	24.9	75.2

not the only portion of the tuber that offers resistance to the passage of gases. When gas is withdrawn from a given lot of tubers, with short intervening intervals, the amount extracted at each successive period is less than that from the preceding extraction; this fact suggests also that air cannot freely pass inward without some resistance. The amount of gas withdrawn again from tubers three or four days after peeling, is less than that withdrawn immediately after peeling, but somewhat more than that extracted from unpeeled tubers at the same time. Gas extracted from tubers immediately after peeling has a larger percentage of carbon dioxide than the gas withdrawn from the same lot just before peeling; on the other hand, when gas is extracted twice within a few minutes from the same lot of tubers without peeling or injuring, it has a lower percentage of carbon dioxide at the second extraction than at the first. With these treatments, the percentage of oxygen in the extracted gas does not change very much but usually decreases slightly in peeled tubers; with unpeeled tubers it increases somewhat in the extraction immediately after the first. Gases extracted and analyzed from peeled tubers three or four days after peeling have a higher carbon dioxide content and a somewhat higher oxygen content than those extracted from unpeeled tubers at the same time.

TABLE 19

EFFECT OF PEELING ON AMOUNT AND COMPOSITION OF GAS EXTRACTED FROM
WHITE ROSE TUBERS; FEBRUARY 25Twelve tubers in each lot; weight 266 grams; stored at 25° C; average
of duplicate samples

Treatment	Gas extracted, cc	Composition of interior gas, per cent		Total CO ₂ plus O ₂	Per cent N ₂ , by difference
		CO ₂	O ₂		
Lot 3 {	Before peeling.....	6.15	11.5	22.4	77.6
	Immediately after peeling.....	6.75	23.0	33.6	66.4
	Four days after peeling.....	4.8	12.2	26.0	74.0
	Not peeled.....	5.95	12.4	23.4	76.6
Lot 4 {	Not peeled (immediately after first extraction)....	4.4	10.2	23.0	77.0
	Not peeled, four days later.....	4.5	11.3	23.9	76.1

TABLE 20

EFFECT OF PEELING ON AMOUNT AND COMPOSITION OF GAS EXTRACTED FROM
IRISH COBBLER TUBERS; FEBRUARY 26Eight tubers in each lot; weight 249 grams; stored 8° to 10° C; average
of duplicate samples

Treatment	Gas extracted, cc	Composition of interior gas, per cent		Total CO ₂ plus O ₂	Per cent N ₂ , by difference
		CO ₂	O ₂		
Lot 5 {	Before peeling.....	6.45	1.8	23.0	77.0
	Immediately after peeling.....	6.45	4.2	23.9	76.1
Lot 6 {	Not peeled.....	6.25	3.5	22.7	77.3
	Not peeled (immediately after first extraction)....	6.20	1.8	23.0	77.0

TABLE 21

EFFECT OF PEELING ON AMOUNT AND COMPOSITION OF GAS EXTRACTED FROM
IRISH COBBLER TUBERS; FEBRUARY 26Eight tubers in each lot; weight 240 grams; stored 8° to 10° C; average
of duplicate samples

Treatment	Gas extracted, cc	Composition of interior gas, per cent		Total CO ₂ plus O ₂	Per cent N ₂ , by difference
		CO ₂	O ₂		
Lot 7 {	Before peeling.....	6.25	3.5	22.5	77.5
	Before peeling (immediately after the first).....	6.20	1.9	22.8	77.2
	Immediately after peeling.....	6.5	4.9	25.2	74.8

DISCUSSION OF RESULTS

Some definite differences in rates of emission of carbon dioxide and absorption of oxygen, composition of interior gas, and permeability of tubers to gas have been found in tubers stored under various conditions and those treated with chemicals. These differences appear to be correlated with the length of the rest period.

Tubers treated with ethylene chlorhydrin and those chemically untreated are, when moist-stored, more permeable to the passage of gas than the chemically untreated dry-stored. Regardless of the method of treatment, the shorter the time between harvesting and the extraction of the gas, the more permeable are the tubers to the gas. The amount of gas extracted from the same lot of tubers also decreases throughout the storage period if the gas is first extracted and the potatoes stored late in the rest period. It was also found that White Rose and Irish Cobbler tubers have a higher respiratory activity when harvested immature, but that this decreases as maturity advances and also during subsequent storage at 25° C. These data suggest that the rate of respiration may be greatly influenced by the permeability of the tuber tissue to carbon dioxide and oxygen.

Appleman and Miller⁽²⁾ suggest that the higher respiration in immature Rural New Yorker potatoes for a period after digging may result from the fact that the skins are more permeable to gas. Removing the outer layer from small whole tubers with well developed periderm which was relatively low in permeability to gas, resulted in an increase in amounts of gas extracted similar to the increase in the case of the tubers which earlier during the rest period were chemically treated or stored moist. Three or four days after peeling, when the wound periderm had formed, the gas extracted from the peeled tubers decreased in quantity almost to the same level as that from unpeeled tubers. Analyses of these extracted gases indicate that the wound periderm that formed on the peeled tuber is similar to the periderm of the unpeeled tubers in its permeability to carbon dioxide and oxygen.

The increase in carbon dioxide immediately after peeling and the slight decrease in oxygen may be the result of increased respiration from wounding. This hypothesis does not appear plausible, however, because of the very short interval between peeling and the extraction of the gas. Stich⁽³⁰⁾ and Johnstone⁽¹⁵⁾ have shown that the increase

in rate of carbon dioxide given off after wounding largely results from mechanically facilitating the exchange of gases. The results of this investigation also suggest that the periderm of the tuber is more permeable to oxygen than to carbon dioxide, because the increase in percentage of carbon dioxide found is several times the decrease noted in oxygen. The data on unpeeled tubers with gas withdrawn again immediately after the first extraction suggest this also, for the carbon dioxide is lower and the oxygen percentage is higher in the second extraction than in the first.

This supposition is not borne out, however, by the studies on rates of diffusion of dissolved oxygen and carbon dioxide. Gases may, however, diffuse either in the dissolved or in the undissolved state. In the dissolved state, carbon dioxide would, because of its higher coefficient of solubility, diffuse at a greater rate than oxygen. The periderm of the potato tuber is, however, extremely dry, corky, and impervious to water. If the passage of gas through this tissue were in the undissolved state, oxygen would diffuse faster than carbon dioxide. The data of these experiments suggest that the passage of gas through the well-developed periderm of potato tubers may be at least partially in the undissolved state.

The work of Becquerel⁽⁷⁾ shows that thoroughly dried seed coats of certain plants are impervious to various gases, and Shull⁽²⁷⁾ states that no evidence was obtained of the diffusion of oxygen through absolutely dry seed coats of *Xanthium*. Similar data have been presented by Crocker,⁽⁹⁾ Shull,⁽²⁶⁾ and others working with seeds possessing unusually long rest periods. They found that the removal of the seed coats of *Xanthium* seeds induced oxygen entrance and germination to occur much sooner than when the seed coats were intact. Shull⁽²⁸⁾ also found that increased oxygen pressure caused a large increase in the oxygen intake with the coats of *Xanthium* intact.

Investigation at this experiment station showed that potato tubers in gas of 60 per cent oxygen for a period of 48 hours absorbed more of this gas than those in air. This increase was not very great—about 1–2 milligrams per kilogram per hour. Perhaps a 48-hour exposure so late in the rest period is too brief to cause greater response. In other experiments in which tubers in the latter part of the rest period were kept in gas of 60 per cent oxygen, there was no apparent abbreviation of the rest period. Favorable results with high oxygen percentage might, however, be obtained if the tubers were exposed to the oxygen earlier in the rest period.

One should note that in all experiments of this investigation there is a larger oxygen absorption by the tubers subjected to those treat-

ments and conditions which shorten the rest period. This increased absorption of oxygen may be due, at least partially, to the increased permeability of the periderm to this gas. Conversely, the low permeability of the tissue to carbon dioxide probably plays a role in the metabolic processes of the tuber by the accumulation of this gas

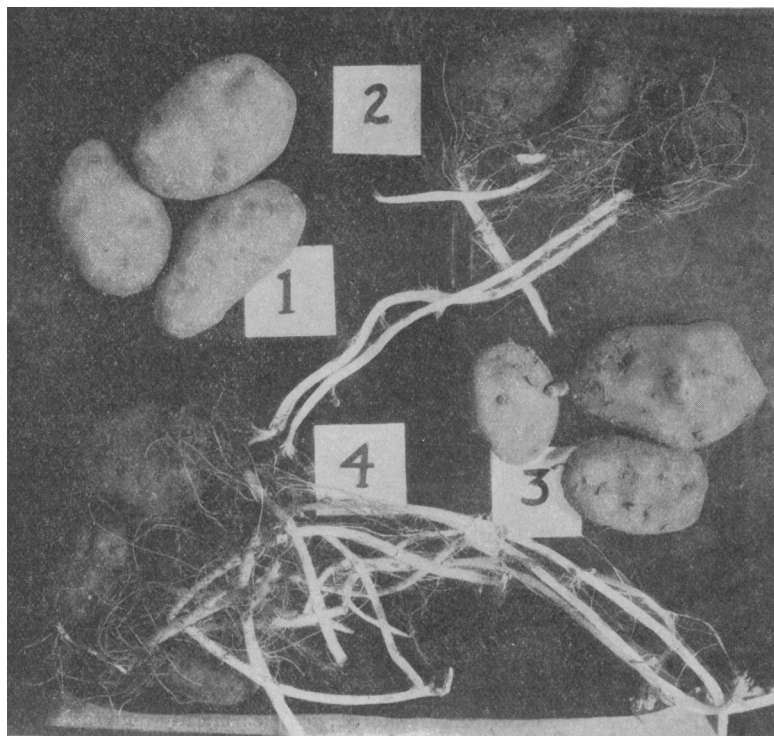


Fig. 4. White Rose potato tubers in 25° C storage, harvested November 10, treated November 28-29, stored November 29, 1928, and photographed January 15, 1929. (1) Chemically untreated, dry-stored; (2) chemically untreated, moist-stored; (3) ethylene-chlorhydrin-treated, dry-stored; (4) ethylene-chlorhydrin-treated, moist-stored. Note the dark color of the periderm and the prominent lenticels in the moist-stored tubers.

which may result in prolonging the rest period. Magness and Diehl⁽¹⁹⁾ are of the opinion that there may be a limitation in the oxygen supply which retards ripening of apples, or an increase in carbon dioxide which may inhibit or stop oxidation and further ripening. Willaman and Beaumont⁽³²⁾ also state that an accumulation of carbon dioxide in the atmosphere surrounding plant tissue appreciably affects the respiration of that tissue. Mack⁽¹⁷⁾ also has shown that after celery has been treated with ethylene, the removal of carbon dioxide by a solution of potassium hydroxide increases the rate of blanching.

Appleman⁽¹⁾ states that the treatments that shorten the rest period cause an increase in oxygen absorption; but he drew this conclusion only from the amount of carbon dioxide given off. Results of experiments with moist tubers, however, indicate that at least for short periods of time, the rate of carbon dioxide loss is not a reliable criterion for determining the amount of oxygen absorbed.

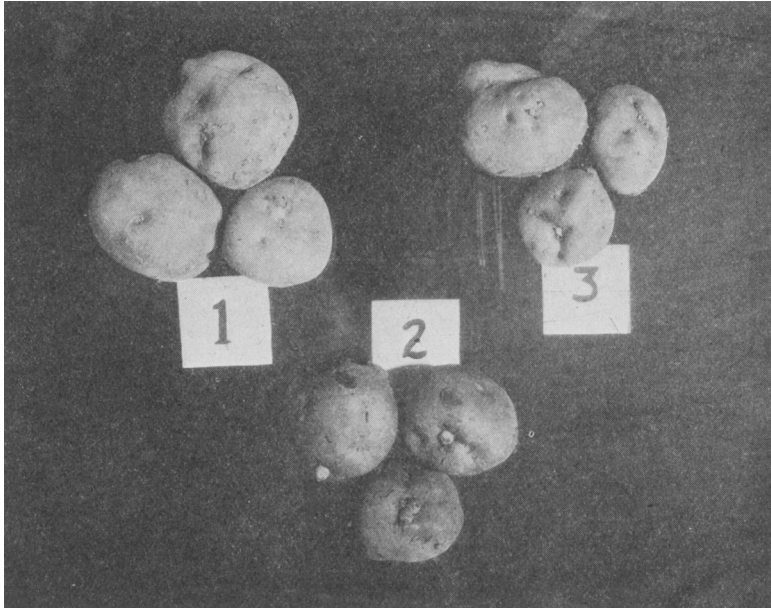


Fig. 5. Irish Cobbler potato tubers in 25° C storage, harvested November 10, treated December 10-11, stored December 11, 1928, and photographed January 15, 1929. (1) Chemically untreated, dry-stored; (2) chemically untreated, moist-stored; (3) ethylene-chlorhydrin-treated, dry-stored. Note the dark color and large, stubby sprouts of the untreated moist-stored tubers.

Moist storage of potato tubers as a means of abbreviating the rest period has not long been advocated. Rosa⁽²⁴⁾ states that moist storage, especially at moderate temperatures, has greatly shortened the rest period. Loomis,⁽¹⁶⁾ however, has concluded that at moderate temperatures the rest period was not shortened by storing potatoes in moist moss. In the investigations of the writer, however, moist storage at 25° C was one of the most effective methods of breaking the rest period. The behavior of moist-stored tubers, with regard to gaseous exchange and gaseous content, has been compared with that of tubers chemically treated and chemically untreated and stored dry. All lots of tubers stored moist have a greater rate of emission of carbon dioxide and absorption of oxygen than those stored dry. The

longer the time between harvest and moist storage, the longer it takes for the loss of carbon dioxide and absorption of oxygen to begin increasing and to reach the maximum rate.

When tubers were chemically treated and stored moist, the effects of both treatments were evident in rate of loss of carbon dioxide and absorption of oxygen. Keeping tubers in moist media facilitates the movement of carbon dioxide and oxygen through the periderm, apparently by increasing the permeability to these gases. These data suggest also that the increased rate of loss of carbon dioxide is a direct result of the increased absorption of oxygen. The data of the experiments in which the tubers were in the jar for a period of only 48 hours, show a much higher rate of absorption of oxygen by the moist than by the dry tubers, but only a small increase in rate of loss of carbon dioxide by the moist over those of dry storage. Analyses of the interior gas show, however, that within these 48 hours metabolic action has increased, as is manifested by the higher carbon dioxide and somewhat lower oxygen content in the moist than in the dry tubers. A longer exposure in the moist media would very likely result in a more rapid loss of carbon dioxide. In other experiments, tubers kept continuously moist for several weeks show a much increased rate of carbon dioxide loss parallel with the higher rate of absorption of oxygen.

The combined data of these two series of experiments indicate further that moist-stored tubers are at first more permeable to oxygen than the dry-stored; then follows a period when the differences decrease, and then a period when those stored moist continue to gain over those stored dry with both carbon dioxide and oxygen. Perhaps at the beginning of the experiments, when the moisture has not yet had sufficient time to penetrate the periderm, the two gases diffuse through only or mainly in the undissolved state. In this case, oxygen would pass through more rapidly than carbon dioxide. Later, however, when the moisture has penetrated the periderm, the gases will tend to diffuse through in the dissolved state. Carbon dioxide should then pass through the more rapidly. The amount of oxygen absorbed by the dry-stored lots decreases during storage, whereas that of the moist-stored lots increases. The partial pressure differences of the gases inside and outside of the tubers probably would account for some of these results, but data of those experiments in which a solution of potassium hydroxide was placed in the respiration jars, indicate that these differences do not result entirely from changes of partial pressure.

Tubers treated with ethylene-chlorhydrin and stored dry show behavior similar to that of the chemically untreated, moist-stored

tubers except that the former are usually more rapid in their action immediately after treatment and storage and that after the initial rise they gradually decline to a lower level than the action of the chemically untreated, moist-stored and ethylene-chlorhydrin-treated, moist-stored lots.

Tubers of the ethylene-chlorhydrin-treated, moist-stored lots had the shortest rest period. Next in order followed the chemically untreated, moist-stored, the ethylene-chlorhydrin-treated, dry-stored, and the chemically untreated, dry-stored, when all were stored at 25° C. Photographs of tubers treated in this manner are shown in figures 4 and 5.

SUMMARY AND CONCLUSIONS

White Rose and Irish Cobbler tubers were used in an attempt to ascertain how various treatments affect the rate of loss of carbon dioxide and absorption of oxygen, the composition of interior gas of the tubers, the permeability of the periderm to gases, and the length of the rest period. The treatments included harvesting at various stages of maturity, subjection to ethylene chlorhydrin vapor for 24 hours, storage dry and storage moist, storage in air of high oxygen percentage, and peeling the tubers.

Irish Cobbler tubers were dug at various stages of maturity on May 21 and 31, June 11 and 21, and July 2; the White Rose tubers were dug on the same dates as the Irish Cobbler and also on July 12.

Chemically treated tubers were subjected to 0.75 cc of 40 per cent ethylene chlorhydrin per liter of space for 24 hours.

Tubers of the dry-stored lots were stored in shallow wooden trays; those of the moist-stored lots, in wooden boxes in well-leached moist sphagnum moss or coarse, moist sawdust.

Dry and moist tubers were placed in respiration jars containing air with 20.6 per cent and 60.0 per cent oxygen with and without the accumulation of carbon dioxide.

The permeability of the periderm of the tubers to gas was determined by withdrawing the gas from the tubers into a vacuum from whole uninjured tubers and from peeled tubers.

The respiratory gases were analyzed for carbon dioxide and oxygen with the Orsat gas analysis apparatus. The gases extracted from the tubers into a vacuum were analyzed for carbon dioxide and oxygen with a modified Henderson's Respiratory Gas Analyzer.

White Rose and Irish Cobbler tubers harvested immature exhibit a higher respiratory activity at time of digging than those harvested more mature. The respiration rate gradually declines with advancing

maturity in the field and in storage at 25° C, although much more rapidly in the latter case. Data on amounts of gas extracted from small whole tubers indicate that the decrease in respiration rate as the maturity and storage periods advance partially results from the increase in development of the periderm as a barrier to the passage of oxygen and carbon dioxide.

White Rose tubers have a higher respiratory activity and a shorter rest period than Irish Cobbler tubers.

Treating tubers with ethylene chlorhydrin and keeping them in moist storage tend to abbreviate the rest period and cause a striking increase in rate of loss of carbon dioxide and absorption of oxygen over the chemically untreated, dry-stored tubers.

Analyses of interior gases in relation to the rate of carbon dioxide loss and oxygen absorption indicate that chemical treatments and moist storage facilitate the exchange of gases in potato tubers.

Tubers stored moist at 25° C in jars of air and of 60 per cent oxygen, absorbed much more oxygen than dry-stored tubers, but gave off only slightly more carbon dioxide during a 48-hour period. The presence of a solution of potassium hydroxide in the jars increased the absorption of oxygen by the tubers. Tubers in an atmosphere of 60 per cent oxygen absorbed slightly more of this gas than those in air. The relation of the composition of the interior gas to the above treatments also indicates that moist tubers are more permeable to carbon dioxide and oxygen than dry tubers.

Results of amounts of gas extracted from small, whole White Rose tubers indicate that the chemically treated and moist-stored tubers are more permeable to gas than the chemically untreated dry-stored tubers. All tubers become less permeable to gas as the period between harvest and extraction increases.

Comparisons of the amount and composition of the gas extracted from peeled and unpeeled whole tubers indicate that the periderm offers resistance to the passage of carbon dioxide and oxygen, also that the interior tissue of the tubers retards somewhat the passage of these gases.

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The titles of the Technical Papers of the California Agricultural Experiment Station, Nos. 1 to 20, which HILGARDIA replaces, and copies of which may be had on application to the Publication Secretary, Agricultural Experiment Station, Berkeley, are as follows:

1. The Removal of Sodium Carbonate from Soils, by Walter P. Kelley and Edward E. Thomas. January, 1923.
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