STUDIES OF ONION ROOT RESPIRATION*

IV. KINETICS OF THE RESPIRATORY OVERSHOOT**

by

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INTRODUCTION AND METHODS

LUND[1, 2] and LUND AND ROSENE[3] in explaining a rebound observed in the E.M.F. of frog skin, Douglas fir, and root tips of *Allium cepa* when the environment was changed from one of high oxygen tension to one of low oxygen tension (or in the case of the Douglas fir, when the temperature of the surroundings was subjected to wide variation), attributed this rebound[1] to "accumulation of oxidizable substances during the periods in absence of oxygen or in low oxygen tension, and their increased rate of removal by oxidation upon readmission of oxygen". BURTON[4] in a theoretical analysis of overshoot phenomena has indicated that from a kinetic standpoint, the reaction rate constant involved is of the first order. He extended his treatment to show that a diffusion reaction is chiefly concerned. The work to be described in this paper was performed with the hope of demonstrating experimentally that there is an accumulation of oxidizable substances during an anaerobic period which are removed by a reaction of the first order when oxygen is readmitted to the respiring system.

Use was made of root segments of *Allium cepa* grown under conditions previously described[5, 6, 7]. The method of measurement was that of amperometric titration explained in detail in another place[8]. Two-day old root segments, either from the 0–5 mm portion (the mitotically active tip) or the 10–15 mm portion (the differentiated region) were suspended in phosphate buffer of p_H 6.48 which had been saturated with oxygen at the temperature to be employed in the measurements (15, 20, 25, 30, 35, or 43°C). The suspended roots were placed in a modified duBuy-Olson cell and a dropping mercury electrode inserted into the cell. The anode was a still pool of mercury. Voltage was applied gradually through the range 0.0–0.5 V. At this point the polarization proper was stopped and the diffusion current, due to the discharge of oxygen was recorded by means of the Leeds and Northrup Micromax recorder. The fall in current was related directly to the fall in concentration of oxygen, *i.e.*, directly to the consumption of oxygen

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by the root segments. After a short interval the oxygen saturated buffer was swept from the cell and replaced by an oxygen-free solution. The recording instrument showed the residual current of the system. When the tissue had been anaerobic for the desired period (from 5 to 45 minutes) the solution was again removed and replaced by one with a high oxygen tension. The course of oxygen consumption now indicated by the fall in diffusion current showed the rebound respiration.

RESULTS

Initial Respiration

It was found that the initial respiration of onion root segments under the conditions mentioned above is of the zero order with respect to oxygen. This is in direct agreement with the findings of WANNER[9], of BERRY[6], and of BERRY AND NORRIS[10]. WANNER reported this type of behaviour for a single root down to very low oxygen tensions. BERRY AND NORRIS have been able to define the critical oxygen tension at various temperatures.

Table I shows the zero order reaction rate constants for both segments at all temperatures under investigation. Lack of reproducibility has been explained by the presence of the plastic inset in the electrolysis vessel for the support of the root segments[8].

TABLE I

ZERO ORDER REACTION RATE CONSTANTS

t °C	0–5 mm Root Segments $k_0 \cdot 10^6$	10–15 mm Root Segments $k_0 \cdot 10^6$	t °C	0–5 mm Root Segments $k_0 \cdot 10^6$	10–15 mm Root Segments $k_0 \cdot 10^6$
15	2.354	2.114	30	1.712	1.310
	1.661	0.876		2.709	0.755
	0.866	0.829		0.638	1.496
20	1.703	0.894		2.129	1.446
	1.010	0.995		1.661	
	0.332		35	1.128	1.901
25	1.073	0.792		1.520	1.168
	0.675	0.621		0.684	0.741
	0.318	0.437		1.928	0.400
	0.811	0.747		0.634	2.260
		0.611		2.460	2.080
		0.894		0.779	1.170
30	1.092	2.567		2.074	1.325
	0.852	1.386	43	1.590	1.253
	0.954	0.912		0.350	0.634
	1.845	1.526		0.513	0.502
	0.459	1.132			

Rebound Respiration

Respirations after varying periods of anaerobiosis were likewise measured for both root segments under the conditions described. In most cases it was found that the data were best represented by a plot of the first order with respect to oxygen. Fig. 1 shows the general appearance of these curves. The units are log of the apparent oxygen concentration (for explanation see[8]) of the solution against time in seconds after the introduction of the second aerobic solution. The break in the curve with the attendant rapid change

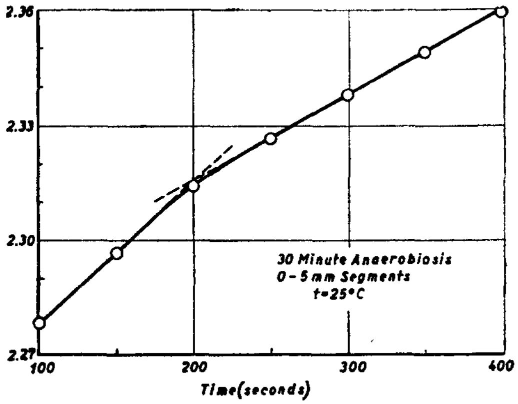

Fig. 1. First Order Plot of Typical Rebound Reaction

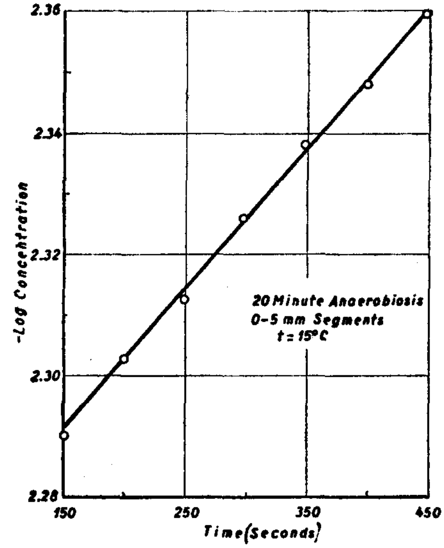

Fig. 2. Anomalous First Order Plot for One Rebound Reaction

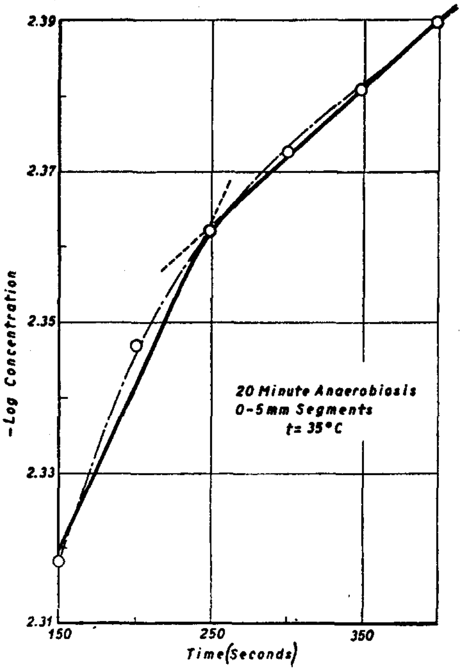

Fig. 3. Explanation in Text

in slope was found to be characteristic of every overshoot reaction save that for the 0–5 mm segments at 15°C after 20 minutes of anaerobiosis. Tables II and III contain the values found for the first order reaction rate constants for the 0–5 mm and the 10–15 mm segments, respectively, at all temperatures. The constant corresponding to the left hand portion of the curve is designated as k_{I}, to the right hand portion, as k_{II}. The single case where only one k was obtained, as mentioned above, was designated as k_{I}. For reasons which will be discussed later it may be that it should have been classified as the k_{II} portion of the respiration. The curve for this is shown in Fig. 2. For some few of the reactions obtained the data seemed best represented by a curve rather than two straight lines. This type of result is shown in Fig. 3. In most cases, however, the drawing of two straight lines gave the best fit. For that reason, all data were treated in this fashion.

The magnitude of the rebound reaction was roughly a function of the length of anaerobiosis preceeding it, up to a certain maximum time, after which the rebound disappeared completely or nearly completely. This is shown by the data in Table IV, which give the times necessary for the disappearance of the overshoot.

While the zero order respiration was in itself not a reproducible measurement, the relative magnitude of the first order respiration constants did not seem to be affected

TABLE II

FIRST ORDER SPECIFIC REACTION RATE CONSTANTS 0–5 mm ROOT SEGMENTS

t°C	k_I Length of Anaerobiosis (minutes)					
15	20 $+5.182\cdot10^{-4}$	30 $+2.211\cdot10^{-3}$	45 $+8.291\cdot10^{-4}$			
20	10 $+7.649\cdot10^{-4}$ $+7.340\cdot10^{-4}$	20 $+1.01\cdot10^{-3}$				
25	10 $+3.931\cdot10^{-3}$	20 $+1.309\cdot10^{-3}$	30 $+8.824\cdot10^{-4}$ $+8.291\cdot10^{-4}$			
30	2 $+8.41\cdot10^{-4}$ $+7.00\cdot10^{-4}$	10 $+1.75\cdot10^{-3}$	15 $+4.00\cdot10^{-4}$ $+4.80\cdot10^{-4}$	20 $+1.33\cdot10^{-3}$	25 $+1.20\cdot10^{-3}$	30 $+4.26\cdot10^{-4}$
35	2 $+1.075\cdot10^{-3}$ $+1.382\cdot10^{-3}$	10 $+1.693\cdot10^{-3}$ $+1.534\cdot10^{-3}$	15 $+1.534\cdot10^{-3}$ $+1.692\cdot10^{-3}$	20 $+1.935\cdot10^{-3}$		
43	10 $+1.842\cdot10^{-4}$	15 $+2.064\cdot10^{-3}$	20 $+2.687\cdot10^{-3}$			

t°C	k_{II} Length of Anaerobiosis (minutes)					
15	20 —	30 $+9.212\cdot10^{-4}$	45 $+4.606\cdot10^{-4}$			
20	10 $+9.000\cdot10^{-4}$ $+9.519\cdot10^{-4}$	20 $+8.970\cdot10^{-4}$				
25	10 $+9.212\cdot10^{-4}$	20 $+5.007\cdot10^{-4}$	30 $+5.234\cdot10^{-4}$ $+4.606\cdot10^{-4}$			
30	5 $+3.00\cdot10^{-4}$ $+4.00\cdot10^{-4}$	10 $+4.28\cdot10^{-4}$	15 $+2.40\cdot10^{-4}$ $+2.85\cdot10^{-4}$	20 $+3.11\cdot10^{-4}$	25 $+2.00\cdot10^{-4}$	30 $+2.00\cdot10^{-4}$
35	5 $+9.212\cdot10^{-4}$ $+9.212\cdot10^{-4}$	10 $+7.197\cdot10^{-4}$ $+9.673\cdot10^{-4}$	15 $+6.149\cdot10^{-4}$ $+2.303\cdot10^{-4}$	20 $+4.168\cdot10^{-4}$ $+4.113\cdot10^{-4}$		
43	10 $+3.943\cdot10^{-4}$	15 $+8.880\cdot10^{-4}$	20 $+1.152\cdot10^{-4}$			

TABLE III

FIRST ORDER SPECIFIC REACTION RATE CONSTANTS
10–15 mm ROOT SEGMENTS

t°C	k_I Length of Anaerobiosis (minutes)				
15	20 —	30 $+6.448\cdot 10^{-4}$	45 $+1.013\cdot 10^{-3}$		
20	10 $+4.370\cdot 10^{-4}$	20 $+9.090\cdot 10^{-4}$			
25	10 $+2.879\cdot 10^{-3}$	20 $+1.819\cdot 10^{-3}$	30 $+5.758\cdot 10^{-4}$		
30	10 $+7.00\cdot 10^{-4}$ $+4.580\cdot 10^{-4}$	15 $+5.80\cdot 10^{-4}$ $+5.00\cdot 10^{-4}$	20 $+8.00\cdot 10^{-4}$ $+8.08\cdot 10^{-4}$	25 $+7.00\cdot 10^{-4}$	30 $+4.02\cdot 10^{-4}$
35	5 $+3.915\cdot 10^{-3}$	10 $+1.290\cdot 10^{-3}$ $+1.152\cdot 10^{-3}$ $+1.198\cdot 10^{-3}$	15 $+1.201\cdot 10^{-3}$ $+1.996\cdot 10^{-3}$	20 $+1.355\cdot 10^{-3}$	
43	10 $+1.842\cdot 10^{-3}$	15 $+1.053\cdot 10^{-3}$	20 $+1.318\cdot 10^{-3}$		

t°C	k_{II} Length of Anaerobiosis (minutes)				
15	20 —	30 $+4.606\cdot 10^{-4}$	45 $+4.606\cdot 10^{-4}$		
20	10 $+3.000\cdot 10^{-4}$	20 $+7.500\cdot 10^{-4}$			
25	10 $+1.612\cdot 10^{-3}$	20 $+6.149\cdot 10^{-4}$	30 $+3.839\cdot 10^{-4}$		
30	10 $+2.220\cdot 10^{-4}$ $+1.660\cdot 10^{-4}$	15 $+2.850\cdot 10^{-4}$ $+1.250\cdot 10^{-4}$	20 $+2.120\cdot 10^{-4}$ $+4.090\cdot 10^{-4}$	25 $+3.000\cdot 10^{-4}$	30 $+2.280\cdot 10^{-4}$
35	5 $+6.659\cdot 10^{-4}$	10 $+5.527\cdot 10^{-4}$ $+4.606\cdot 10^{-4}$ $+1.152\cdot 10^{-4}$	15 $+3.455\cdot 10^{-4}$ $+7.197\cdot 10^{-4}$	20 $+3.385\cdot 10^{-4}$ $+3.431\cdot 10^{-4}$	
43	10 $+8.061\cdot 10^{-4}$	15 $+5.758\cdot 10^{-4}$	20 $+6.494\cdot 10^{-4}$		

by this defect. Table V shows the result of calculations for the per cent increase in oxygen consumption for the first two 50 second intervals of experimentally measurable rebound for various temperatures and different lengths of anaerobiosis. The reproducibility is good when calculated in this way, in spite of the wide variation of the initial zero order values of the respiratory rate (cf. Table I and also[8]).

TABLE IV

LENGTH OF TIME OF ANAEROBIOSIS NECESSARY FOR THE DISAPPEARANCE OF THE REBOUND REACTION (pH = 6.489)

t°C	Length of Anaerobiosis (minutes)	
	0–5 mm segments	10–15 mm segments
15	Some overshoot after 45	45
25	25	30
30	25	25
35	20	20

TABLE V

REPRODUCIBILITY OF ZERO ORDER REACTION RATE CONSTANT AND OF PERCENT INCREASE IN OXYGEN CONSUMPTION OF INITIAL REBOUND

k_0	% Increase in Oxygen Consumption in the First Measurable 150 Seconds of Second Aerobiosis	Segment toC	Length of Anaerobiosis (minutes)
$1.712 \cdot 10^{-6}$	674	0–5 mm 30	15
$2.709 \cdot 10^{-6}$	645	0–5 mm 30	15
$8.520 \cdot 10^{-7}$	1360	0–5 mm 30	20
$9.540 \cdot 10^{-7}$	1250	0–5 mm 30	20
$0.912 \cdot 10^{-6}$	1108	10–15 mm 30	15
$1.526 \cdot 10^{-6}$	992	10–15 mm 30	15
$1.707 \cdot 10^{-6}$	540	0–5 mm 20	10
$3.320 \cdot 10^{-7}$	565	0–5 mm 20	10

Critical Increment of the Overshoot Reaction

In order to determine the "Biological critical increment" involved in the rebound reaction, plots were made of log k_I and log k_{II} for constant anaerobic periods against the reciprocal of the absolute temperature. These two plots have slopes corresponding to 7500 cal in the case of the 0–5 mm segment (k_I) after 20 minutes of anaerobiosis and 17,800 cal (k_{II}), found after 15 minute anaerobiosis of the segment. Only in the two cases reported did this type of plot lead to a straight line; calculation of the slope was performed according to the ARRHENIUS equation. It is interesting to note in this connection that one of the points on the k_I-curve, namely, that for the determination at 15° C (Fig. 2), did not fall on the line. This point corresponds to that overshoot reaction representable only by one first order curve. It may be that the k-value actually corresponds to that of k_{II} rather than the k_I reported. It is probably fortuitous that connection of the first two points (15 and 20°C) leads to a line of slope nearly that of the k_{II} graph.

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Repayment of the Anaerobically Incurred Oxygen Debt

Calculations were made to determine what amount of the "oxygen debt" incurred during anaerobiosis was repaid in the post-anaerobic period. From the second aerobic respiration curve (that is, that corresponding to the post-anaerobic period) there was subtracted the curve of normal aerobic respiration for the test period in question. For the reasons previously indicated[8] the data were felt to be valid only after the first 150 seconds of aerobiosis had elapsed. In order to estimate the total amount of oxygen consumed, the curves were extrapolated back to zero seconds of aerobiosis. This extrapolation was carried out by assuming that the first 50 seconds of the valid portion of the oxygen consumption curve determined the position of the extrapolated line. The values were read from the center of each 50 second time interval on the graph. Obviously such an extrapolation is not without objection, for it assumes, first, that the amount of oxygen consumed decreases linearly with time over each 50 second interval and second, that the high rate of oxygen consumption begins as soon as the onion roots are placed in the high oxygen environment.

Inasmuch as integration beneath these curves would present great difficulty, the total amount of excess oxygen consumed was determined by calculation. It was further assumed that the midpoint of each 50 second time interval gave the average amount of excess oxygen consumed during that time interval of the post anaerobic reaction. These midpoints (including the values obtained by extrapolation) were summed arithmetically for the total time the overshoot reaction prevailed. From the value obtained in this fashion there was subtracted the value corresponding to the total amount of oxygen that would have been consumed had the products of aerobic metabolism accumulated during the anaerobic period at the rate prevailing during the initial period of respiration; that is to say, the zero order reaction rate constant was multiplied by the length of the anaerobic period in seconds and the value so obtained was the one subtracted. It was found that the amount of oxygen consumed in the second aerobic phase of the respiration was usually many times in excess of that that would have been consumed by the accumulation of aerobically produced intermediates. The greater absolute portion of the excess oxygen consumed

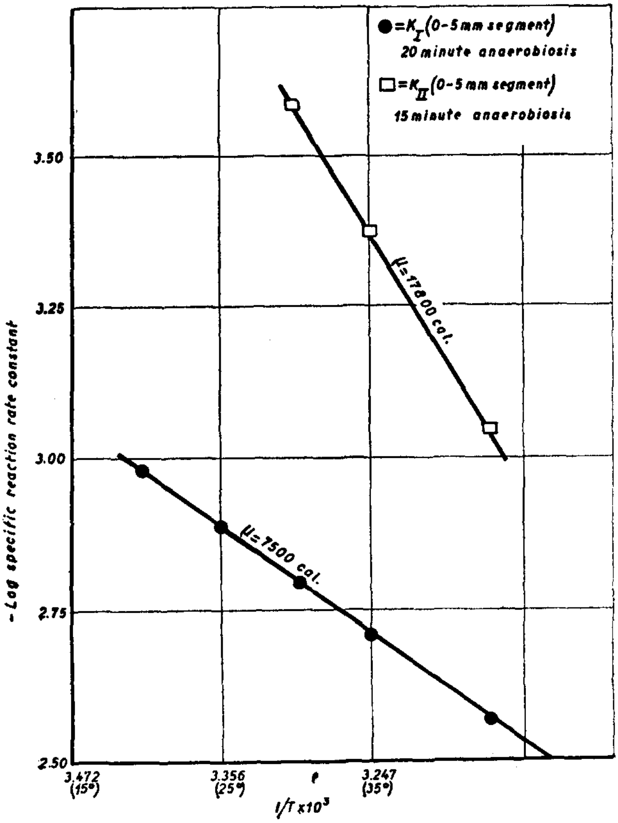

Fig. 4. Arrhenius Plot of Rebound Reaction Rate Constants for Constant Periods of Anaerobiosis

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arises from the extrapolation. However, the course of the extrapolation (as indicated above) is determined uniquely by the position of the overshoot reaction curve, so that the relative orders of magnitude are of interest.

Figs. 5 and 6 show the results of such calculations. In Fig. 5 there is plotted the total amount of excess oxygen consumed in the post-anaerobic period against length of the anaerobic period in minutes at the temperatures 15, 25, 35 and 43°C for the 0–5 mm portion. Fig. 6 shows the same type of plot for the 10–15 mm segment of the root. These graphs show clearly the loss of the detectable rebound reaction for the various temperatures: thus, in the 0–5 mm segments, detectable overshoot had disappeared after approximately 25 minutes of anaerobiosis at 25°C and after 20 minutes at 35°C. A detectable rebound did not appear at 15°C until after a 20 minute period; after about 50 minutes it had disappeared completely. The 10–15 mm portion of the root lost a detectable overshoot after 20 minutes of anaerobiosis at 35°C and after about 30 minutes at 25°C, and after 43 minutes at 15°. For both segments there was no detectable rebound after 30 minutes of anaerobiosis at 43°C. A comparison of the two figures shows a close similarity between the behaviour of the apical and basal segments with respect to the times of appearance and disappearance of the rebound as related to temperature. It is also apparent that the total amount of excess oxygen consumed is greater in the apical segment at all temperatures except 25°C. There is no explanation for this exception. It has also been observed that more acid buffering solutions tend to prevent the loss of overshoot. This will be the subject of a subsequent paper.

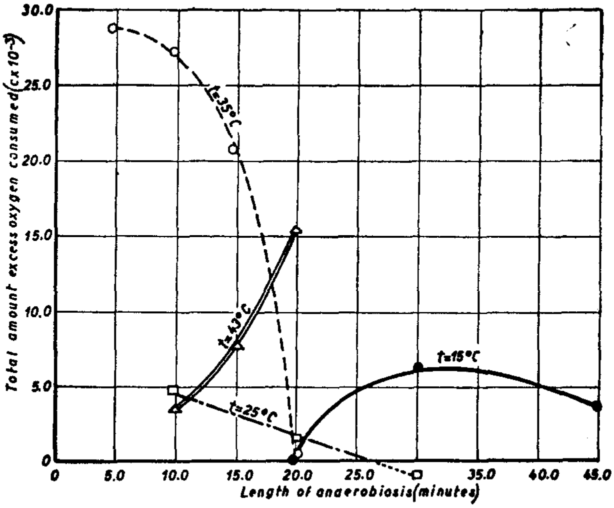

Fig. 5. Total Amount of Excess Oxygen Consumed in Post-Anaerobic Period Against Length of Time of Anaerobic Period in Minutes for the 0–5 mm Root Segment

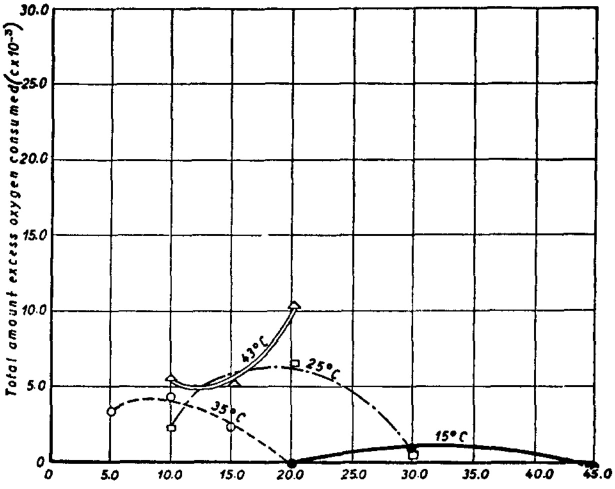

Fig. 6. Total Amount of Excess Oxygen Consumed in Post-Anaerobic Period Against Length of Time of Anaerobiosis in Minutes for the 10–15 mm Root Segment

DISCUSSION

Demonstration of the first order reaction in the rebound is in good agreement with the theoretical treatment of BURTON[4], for he stated that an overshoot may be visualized as a change in the flux equilibrium caused by a shift in the values of the reaction rate constants of diffusion. To be sure, diffusion reactions are generally of the first order. However, if a diffusion reaction is characterized by an energy of activation of the order of 5000 calories, then the energies obtained as critical increments do not completely support his argument that the constant involved is that of diffusion alone. The first portion of the overshoot reaction in the 0–5 mm root segment has a critical increment close to that necessary for diffusion to be the "master process". The second, slower portion of the rebound for this same segment seems to require an energy of activation far in excess of the 5000 calories. A critical increment of 4000 cal for onion root tissue when diffusion is the limiting factor has been reported[10].

All of the experimental findings seem to point to the fact that the rebound reaction as here investigated is actually composed of two different reactions. It might be that the portions of the kinetic curves designated by k_{I} and k_{II} correspond to the same pair of reactions proceeding in each case with different total critical increments. This would seem probable in view of the fact that concentrations are falling rapidly, and, therefore, the probability of reaction is changing quickly because the randomness of the system is varying. More experimental work concerned with the role of substrate in this particular respiration reaction will have to be available before definite assertions are made in this area. The demonstration of an overpayment of the anaerobically produced oxygen debt sometimes many times greater than would be expected on the basis of the accumulation of aerobic metabolites alone affords further indication of the existence of at least two reactions occurring in the post anaerobic respiratory phase. On the basis of the previous theoretical treatment[11] it may well be that the two reactions concerned are: 1) an oxidation of accumulated aerobic metabolites and 2) an oxidation of cumulated products of anaerobic respiration. Whether these processes are both dominated by the velocity of diffusion of oxygen to the oxidation sites, or whether only one of them is, cannot be definitely stated on the basis of the present data. It is known[10], however, that the critical pressure of oxygen changes from about 30% oxygen at 25°C to 50% oxygen at 35°. Under the same conditions the volume of oxygen consumed approximately doubles. Inasmuch as the rebound reaction increases the rate of oxygen uptake by approximately ten-fold, it would seem to be pushing the ability of the diffusion process to the limit in order that the high respiratory rate be maintained, in spite of the fact that in this case it was a question of oxygen saturated solutions. It has been suggested that the 7500 cal value represents a "mixture" of diffusion and chemical processes, for similar values were obtained[10] for normal respiration when a value for oxygen tension just below the critical pressure was employed.

Interpretation of results must take into account an additional difficulty introduced by the variation in temperature. It is well known that at temperatures as high as 40°C reversible denaturation of proteins begins[12]. NICKERSON has recently used this fact to account for temperature produced rebounds in yeast[13]. An increase in temperature will act in two ways to change the activity of an enzyme[14]: the one effect is the usual one of accelerating chemical reactions, the other, caused by the denaturation, is that of inhibition, for above a certain limiting temperature the denatured proteins lose their ability to function as enzymes. This occurs for onion root tissue at temperatures as low as 35°C[10]. However, the presence of large amounts of substrate serve to protect the protein from this denaturation. It may be that it is a combination of factors which accounts for the dramatic changes in slope shown in the 43°C measurements. (See Figs. 5 and 6).

Surprisingly enough the position of the break in the first order curve seems to be independent of the time in seconds after the anaerobic period and also of the apparent oxygen concentration. This is true also for the experiments performed in duplicate and triplicate, in which the *k*-values show great similarity. In the case of the rebound reactions at 43°C there seems to be an increase in the time at which the inflection occurs roughly parallelling the increase in the length of anaerobiosis. Reactions at the other temperatures showed no such simple relationship.

Disappearance of the rebound reaction after a critical period may be explained on either physical (diffusion) or chemical (reaction) grounds. NORRIS[15] in a study of the rebound reaction using the methylene blue reduction time technique found that the overshoot persisted even after the root tissue had been exposed to an anaerobic period lasting for more than two hours. This may be due in part to the fact that segments were suspended in a solution which was more acid. As has been indicated already, the more acid p_H's tend to prevent loss of rebound. Earlier work[16] on electrical rebound in the roots of ***Allium cepa*** showed that the observed potential overshoot was roughly proportional to the length of the anaerobic period up to 30 minutes, but that at 45 minutes the value was constant and maximal. This measurement was carried out in such a fashion that the root was surrounded by a gaseous atmosphere. Preliminary experiments, however, from this laboratory indicate that there is a loss of electrical rebound when the root is surrounded by a fluid. The loss of electrical overshoot after a certain critical period of anaerobiosis described in this paper together with the appearance of the constant maximum in the work of BERRY might be explained on the basis of the previous theoretical considerations[11]. If, as anaerobiosis proceeds, the products of aerobic metabolism have accumulated to such concentration that equilibrium has been reached throughout the entire aerobic metabolic pathway, and if the anaerobic pathway has been called into play, the overshoot reaction should measure the oxygen consumption of both the aerobic and anaerobic products. If the products of anaerobiosis have accumulated to such an extent that the anaerobic pathway likewise has assumed its own equilibrium position, a maximum rebound is understandable, providing that these accumulated products are not lost, either by diffusion, or consumed by chemical reaction. Performance of a rebound measurement in a liquid medium surrounding the roots provides a mechanism for the removal of metabolites by diffusion, if permeability has been altered to such an extent by anaerobiosis that a "leaky" system develops once a sufficient concentration is reached. Some small evidence has been obtained in this direction by means of polarograms which show that the composition of the surrounding solution is changed after long periods of anaerobiosis. Considerable work is indicated here.

Despite the limitations and uncertainties associated with certain phases of this approach to the kinetics of living systems, there seems to be justifiable hope for gaining additional insight into the problem.

SUMMARY

The respiratory overshoot and regular respiration of mitotically active and mature onion root segments have been measured at temperatures ranging from 15 to 43°C. The regular respiration is zero order, the overshoot respiration, of the first order. The rebound reaction seems to be composed of two different reactions, as indicated by the fact that two separate values are obtained for the specific reaction rate constants characterized by different temperature coefficients and by the fact that there is a marked overpayment of the anaerobically incurred oxygen debt. Maxima appear in the total amount of oxygen necessary for the removal of accumulated metabolites in the post-anaerobic reaction. These maxima seem to be a function both of the temperature of the respiring system and of the length of the anaerobic period.

RÉSUMÉ

Nous avons mesuré l'excès respiratoire et la respiration régulière de segments de racines d'oignon mûres et à activité mitotique à des températures allant de 15 à 43°C. La respiration régulière est de l'ordre zéro, la respiration en excès est du premier ordre. Le saut brusque observé au cours de la respiration semble se composer de deux réactions différentes; l'on obtient, en effet, deux valeurs différentes pour les constantes spécifiques de vitesse de réaction caractérisées par des coefficients de température différents; de plus, la dette en oxygène contractée pendant l'anaérobiose est plus que largement compensée. La quantité d'oxygène totale, nécessaire pour faire disparaître pendant la réaction post-anaérobie les métabolites accumulés, montre des maxima qui semblent être fonction de la température du système respirant et de la durée de la période anaérobie.

ZUSAMMENFASSUNG

Der Atmungsüberschuss und die regelmässige Atmung von mitotisch aktiven und reifen Zwiebelwurzelsegmenten wurden bei Temperaturen von 15–43°C gemessen. Die regelmässige Atmung ist nullter Ordnung, die überschüssige Atmung erster Ordnung. Die sprunghafte Änderung der Atmung scheint durch zwei verschiedene Reaktionen bedingt zu sein; dies geht hervor, erstens aus der Tatsache, dass man zwei verschiedene Werte für die spezifischen Reaktionsgeschwindigkeits-Konstanten findet, die durch verschiedene Temperaturkoeffizienten gekennzeichnet sind, und zweitens aus der Tatsache, dass die während der anaeroben Periode entstandene Sauerstoffschuld deutlich überkompensiert wird. Maxima zeigen sich in der Gesamtsauerstoffmenge, welche zur Entfernung der angehäuften Stoffwechselprodukte während der auf die anaerobe Periode folgenden Reaktion nötig ist. Diese Maxima scheinen eine Funktion der Temperatur des atmenden Systems und der Dauer der anaeroben Periode zu sein.

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