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Endogenous Respiration and Polysaccharide Reserves in Baker's Yeast

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In the two following papers an attempt is made to assess quantitatively the Pasteur effect in baker's yeast, to study the effect of a wide range of inhibitors on it, and to determine whether it is related to phosphorylation rates. The present preliminary paper deals with the endogenous metabolism of the same yeast, so that it may be determined to what extent the endogenous metabolism must be taken into account in assessing the results of the experiments on glucose breakdown.

Meyerhof (1925) first observed that the respiratory quotient (R.Q.) of yeast respiring in the absence of added substrate is far below unity (about 0.85), and gave reasons for believing that the R.Q. in the presence of glucose is 1.00. Lundsgaard (1930) demonstrated that in the presence of glucose the apparent R.Q. is 1.00, and remains at that value even in circumstances where there is no possibility of any contribution being made to the carbon dioxide production by a simultaneous fermentation, namely in the presence of 10^{-3} M sodium iodoacetate.

More recently Stier & Stannard (1936) and Spiegelman & Nozawa (1945) have reported that yeast of many varieties, including pure strains of *Saccharomyces cerevisiae*, show an endogenous respiration with an R.Q. of 1.00. This is, of course, taken to imply that the oxidation is one of carbohydrate, i.e. that the yeast is oxidizing its stored polysaccharide; but the same authors show beyond doubt that all the cultures they used are unable to ferment their stored polysaccharide. As yeast contains all the enzymes necessary for both processes, it is difficult to see why the one takes place and the other does not.

MATERIALS AND METHODS

Yeast. A single brand of commercial pressed baker's yeast was used (City Brand Pure Yeast, J. Mann and Co., Leeds). This was made into a suspension in water containing

15 g. fresh wt./100 ml.; for manometric measurements 0.5 or 1.0 ml. was used, according to the metabolic activity of the yeast, in a total volume of 3.0 ml., and for phosphorylation measurements 2.0 ml. in a total of 3.0 ml. (1.0 ml. contained roughly 40 mg. dry wt.)

Measurement of respiration and fermentation. Standard methods, with Warburg manometers, were employed. All manometric measurements were made at 25°, and lasted 1 hr. unless otherwise stated. Whenever a comparison was made between polysaccharide determinations and manometric results, the latter were corrected for processes occurring during the equilibration of the manometers.

All experiments were carried out in 0.016M aminotris-hydroxymethylmethane (tris) buffer at pH 6.5; it was confirmed that there was no change in the CO₂ content of the buffer during fermentation experiments. Aerobic measurements were made in air; the N₂ for the anaerobic experiments was purified by passage over heated copper.

Measurement of polysaccharide content of yeast. The contents of the manometer vessels (3.0 ml.) were treated with 2.0 ml. of 10% trichloroacetic acid and centrifuged. The deposit of yeast cells was hydrolysed in 2.0 ml. of 2N-HCl at 100° for 90–120 min., neutralized and made up to 15 ml., and the glucose content of a measured sample determined by the method of Hanes (1929). The initial polysaccharide content of the yeast was also determined in the same way. The values obtained (total material capable of yielding reducing sugars on acid hydrolysis) will be referred to as 'polysaccharide' and will be expressed as the equivalent amount of glucose.

Table 1. *Respiratory quotient of the endogenous respiration of yeast in different nutritional states*

Figures in parentheses indicate the range of individual values.

Treatment of yeast	No. of samples	R.Q.
Impoverished	6	0.86 (0.82–0.90)
Normal	14	0.86 (0.83–0.91)
Enriched	8	0.83 (0.76–0.90)

Table 2. Q_{O_2} of endogenous respiration and the rate of attack on glucose with yeast in different nutritional states

Treatment of yeast	Polysaccharide content (mg./g. dry wt.)	Q_{O_2}		$Q_{CO_2}^{Na}$	
		Endogenous	In glucose (0.13 %)	Endogenous	In glucose (0.13 %)
Impoverished	271	-4.0	-93	0.1	114
Normal	271	-9.2	-62	0.2	110
Enriched	400	-20.3	-84	0.3	120

Table 3. Absence of loss of polysaccharide during endogenous respiration of yeast

The conditions of the experiments are given in the text.

Expt. no.	Treatment of yeast	Polysaccharide content (mg./g. dry wt.)	Total O_2 consumption (μ l.)	Polysaccharide equivalent of O_2 consumption (mg.)	Polysaccharide (mg./manometer vessel)		
					Before	After	Change
1	Impoverished	271	185	-0.25	11.4	11.4	0
	Normal	271	515	-0.69	11.4	11.3	-0.1
	Enriched	400	961	-1.29	16.8	16.8	0
2	Impoverished	370	200	-0.27	14.5	14.5	0
	Normal	370	330	-0.44	14.5	14.8	+0.3
3	Normal	357	255	-0.34	15.0	15.0	0
4	Enriched	524	1236	-1.66	22.0	22.1	+0.1

Measurement of respiratory quotient. Two pairs of manometers were used, containing yeast suspension and buffer, one pair containing KOH to absorb CO_2 and the other not. The assumption is made that the O_2 consumption is the same in both pairs. Carbon dioxide of fermentative origin need not be considered, as there is no endogenous fermentation.

Measurement of rate of phosphorylation. Baker's yeast as bought contains about 2 mg./g. dry wt. of acid-soluble inorganic P. When glucose is added, the total extractable P remains constant, and the inorganic P level falls (Macfarlane, 1936). A similar fall in inorganic P level is found to occur when yeast is aerated in the absence of any added substrate. The method used to follow these changes was derived from that described in the following paper, in which the phosphorylation was initiated by the addition of glucose, either aerobically or anaerobically. Phosphorylation resulting from endogenous metabolism occurs only aerobically, as there is no anaerobic endogenous metabolism.

A suspension of yeast (2 ml.) was measured into each of a series of 4 in. $\times$ 0.5 in. test tubes with 0.5 ml. of tris buffer, pH 6.5, and 0.5 ml. of water or inhibitor solution. Each tube in turn was vigorously aerated by shaking for the required period, and the reaction then stopped by the addition of 2.0 ml. of 10% trichloroacetic acid solution. After they had stood for about 1 hr. at room temperature the tubes were centrifuged, and the inorganic P content of the supernatant was determined (Fiske & Subbarow, 1925). For comments on the accuracy of this procedure see Stickland (1956b).

Treatment of the yeast. It was possible that the differences in R.Q. reported in the literature might be due to a difference in the nutritional state of the yeast; both Stier & Stannard (1936) and Spiegelman & Nozawa (1945) used fresh cells from young cultures (45 hr. at 25° and 30° respectively), and Meyerhof (1925) used ordinary baker's yeast. For many of the following experiments therefore the yeast suspension

was submitted to one of three treatments: (a) aerated vigorously at either room temperature or at 25° for 3 or 4 hr. (impoverished); (b) left standing undisturbed at room temperature for the same period (normal); (c) treated with one-tenth of its weight of glucose, allowed to ferment for 3 hr. at room temperature or 25°, and washed thoroughly five or six times by centrifuging (enriched).

Expression of results. The metabolic processes of yeast in the absence of an added substrate, in contrast to those in the presence of glucose, do not proceed linearly but steadily decrease in rate. All the values for rates measured manometrically in the present paper are for average rates over the first hour. Rates of phosphorylation are calculated from the time taken to esterify 0.2 mg. of inorganic P/g. dry wt. of yeast (see Stickland, 1956b).

RESULTS

Respiratory quotient. The endogenous R.Q. of the yeast as bought was always found to be well below unity. In fourteen samples the value found was 0.85 ± 0.02 (range 0.83–0.91). This value was not appreciably altered by either impoverishing or enriching the yeast (Table 1). The same specimens of yeast respiring in the presence of glucose (about $7.5 \times 10^{-3} M$) showed an average R.Q. of 1.02.

Respiration and fermentation. The average endogenous Q_{O_2} values for several samples of impoverished, normal and enriched yeast were respectively -3.7, -5.7 and -20.5. Table 2 gives the figures for one experiment, and shows in addition that no anaerobic fermentation occurs in any of these conditions, and that the enzymes concerned in respiration and fermentation of glucose are not largely altered in amount by these treatments.

Polysaccharide content. Polysaccharide estimations were carried out on samples of each kind of treated yeast, both before and after respiration had taken place. Table 3 gives the results of some typical experiments. It will be noted that the polysaccharide content of the yeast was very high (some 30 % of the dry wt.), that it was not decreased by the impoverishing process, but that it was considerably increased by the enriching process. During the respiration a quantity of O_2 was consumed which would represent the utilization of an appreciable part of the polysaccharide, if this were indeed the substrate of the oxidation. Actually, no polysaccharide disappeared from the yeast. It had been observed by Fürth & Lieben (1922) that vigorous aeration of yeast does not reduce its content of polysaccharide (*durch 2.2 % HCl abspaltbarer Zucker*).

Phosphorylation associated with endogenous respiration. Just as when yeast is treated with glucose aerobically there is a rapid O_2 consumption ($Q_{O_2} = -70$) and a very rapid esterification of inorganic P ($Q_P^0 = -120$) (Stickland, 1956*a, b*), so the slower endogenous respiration ($Q_{O_2} = -5$) is associated with a slower rate of phosphorylation ($Q_P^0 = -38$; average of four samples). The whole course of this phosphorylation is shown in Fig. 1; it will be seen that the minimum value for the inorganic P reached, some 60 % of the original resting value, is much higher than when glucose is present (Stickland, 1956*b*). Surprisingly, no difference could be detected in the rates or in the minimum values reached between impoverished, normal and enriched samples (Fig. 1).

Action of inhibitors on the endogenous respiration. The extent of the inhibition of the respiration of this

brand of yeast in the presence of glucose, by a number of inhibitors, is given in the following paper (Stickland, 1956*a*). The endogenous respiration was, in general, less easily inhibited (Table 4); phenylurea had no effect, or sometimes produced a stimulation, at a concentration which caused some 90 % inhibition of the glucose respiration; KCN and sodium azide had to be present at 30–100 times as high a concentration to produce a comparable effect;

Fig. 1. Changes in the inorganic phosphorus content of yeast during endogenous respiration. Δ , Normal yeast, no added substrate; $\times$, impoverished yeast, no added substrate; $\square$, enriched yeast, no added substrate; $\blacktriangle$, normal yeast, glucose added.

Table 4. *Effect of inhibitors on the endogenous respiration of yeast*

Each manometer vessel contained 1.0 ml. of a 15 % suspension of 'normal' yeast.

Inhibitor	Concn. (M)	Q_{O_2}		Inhibition (%)
		No inhibitor	Inhibitor present	
KCN	10^{-4}	-8.4	-4.1	51
	3×10^{-4}	-8.4	-1.6	81
	10^{-3}	-8.4	-1.1	87
Sodium azide	10^{-3}	-6.2	-3.5	43
	10^{-2}	-8.4	-1.2	86
Urethane	0.75	-2.5	-1.4	42
	1.5	-2.5	-0.5	81
	3.0	-2.5	0	100
Phenylurea	2×10^{-2}	-3.3	-3.3	0
Sodium arsenate	10^{-4}	-4.9	-4.3	13
	10^{-3}	-4.9	-4.0	18
	10^{-2}	-4.9	-4.4	11
Sodium iodoacetate	10^{-3}	-4.4	-2.5	43
DNP	10^{-3}	-6.2	-8.2	-33
	3×10^{-3}	-6.5	-7.3	-12
	3×10^{-3}	-7.6	-6.3	17

arsenate and arsenite inhibited very little even at the highest concentration. On the other hand, urethane inhibited the endogenous respiration as much as the glucose respiration, and sodium iodoacetate more so. 2:4-Dinitrophenol (DNP) usually stimulated the endogenous respiration but sometimes at the highest concentration (3×10^{-3} M) it caused slight inhibition.

Action of inhibitors on the endogenous phosphorylation. The same inhibitors inhibited the endogenous phosphorylation to approximately the same extent as the endogenous respiration, with the exception of DNP which suppressed the phosphorylation completely for the first 5 min. (Table 5). This was followed by an extremely slow esterification in the next 20 min. ($Q_P^0 = -0.4$, compared with $Q_P^0 = -34$ in the control).

Action of DNP. Rothstein & Berke (1952) observed that 5×10^{-4} M DNP induced a CO_2 production in yeast anaerobically, and showed that it was partly at the expense of the 'total hydrolysable sugar' fraction of the yeast (in the present paper referred to as 'polysaccharide'). They accepted the conclusion of Spiegelman & Nozawa (1945) and Stier & Stannard (1936) that the endogenous respiration represented an oxidation of glycogen, and deduced that the DNP made the

attack on stored polysaccharide possible under anaerobic as well as aerobic conditions.

It was important to determine whether the R.Q. of the endogenous respiration in the presence of DNP has, under the conditions of the present experiments, the same low value as in its absence. Attempts to measure the R.Q. directly were frustrated by the fact that, as would be expected from the anaerobic experiments of Rothstein & Berke (1952), DNP sets up even aerobically in yeast an evolution of CO_2 of such magnitude that the apparent R.Q. may be as high as 2.0. To determine the nature of the substrate of the CO_2 evolution, determinations were therefore made of the polysaccharide content of the yeast before and after the manometric period, in the presence and in the absence of 3×10^{-3} M DNP; the results of some such experiments are given in Table 6.

It will be seen that polysaccharide did disappear and the quantity so disappearing was enough to account not only for the extra CO_2 production, but also for the O_2 consumption, i.e. in the presence of DNP there was a complete change-over from non-carbohydrate to carbohydrate breakdown. The amount of polysaccharide oxidized and the amount fermented aerobically, under the influence of DNP, both varied widely with the state of nutrition of the

Table 5. *Inhibition of the phosphorylation associated with the endogenous respiration of yeast*

Q_P^0 was determined from the time required for the esterification of 0.2 mg. of inorganic P/g. dry wt. of yeast.

Inhibitor	Concn. (M)	Q_P^0		Inhibition (%)
		No inhibitor	Inhibitor present	
KCN	10^{-4}	-52	-36	29
	5×10^{-4}	-52	-28	46
Sodium azide	10^{-2}	-52	0	100
Urethane	0.75	-52	0	100
Phenylurea	10^{-2}	-52	-31	40
Sodium arsenite	10^{-3}	-52	-62	-20
DNP	10^{-3}	-52	0	100

Table 6. *Effect of DNP on endogenous respiration and aerobic fermentation in yeast*

Expt. no.	Treatment of yeast	Concn. of DNP (mM)	Total O_2 consumed ($\mu\text{l.}$)	Non-respiratory CO_2 produced* ($\mu\text{l.}$)	Polysaccharide equivalent of			Polysaccharide found (mg.)		
					O_2 (mg.)	CO_2 (mg.)	$\text{O}_2 + \text{CO}_2$ (mg.)	Initial	Final	Change
1	Impoverished	0	185	0	0.25	0	0.25	11.3	11.4	+0.1
		3	308	83	0.40	0.33	0.73	11.3	10.7	-0.6
	Normal	0	389	0	0.52	0	0.52	11.2	11.1	-0.1
		3	398	271	0.53	1.09	1.62	11.2	9.6	-1.6
	Enriched	0	961	0	1.29	0	1.29	16.8	16.8	0
		3	886	492	1.19	1.98	3.17	16.9	13.8	-3.1
2	Enriched	0	1053	0	1.41	0	1.41	21.8	21.7	-0.1
		3	730	670	0.98	2.69	3.67	21.8	18.4	-3.4

* In the controls without DNP the absence of anaerobic fermentation was taken throughout to imply an absence of aerobic fermentation. In the experiments with DNP, the results showed that the substrate of the respiration was now carbohydrate, so a value of 1.00 was taken for the R.Q. in evaluating the 'non-respiratory CO_2 '.

yeast. The total rate of catabolism of polysaccharide in the presence of DNP was four to five times as great in enriched as in impoverished samples, although the total polysaccharide content was only roughly 50% higher in the former; this suggests that the rate was determined not by the total polysaccharide present, but by the concentration of one particular fraction of it.

It would have been of interest to confirm the nature of the substrate of the respiration by measuring its R.Q., the fermentative CO_2 production being eliminated by the addition of iodoacetate. This proved impossible, as the CO_2 evolution was not susceptible to inhibition even by 10^{-3}M iodoacetate (Table 7).

This result was so unexpected that it was thought worth while to determine (a) whether the anaerobic fermentation of glucose in the presence of DNP was inhibited by iodoacetate, and (b) whether the much higher concentration of yeast cells used in the absence of glucose was binding much of the iodoacetate and reducing its effective concentration. It was found that anaerobic glucose fermentation was almost as susceptible to iodoacetate in the presence of DNP as in its absence, and that 10^{-3}M iodoacetate caused at least 99% inhibition of glucose fermentation even with 42 mg. dry wt. of yeast/manometer vessel.

Action of DNP anaerobically. Rothstein & Berke (1952) found that anaerobic CO_2 production initiated by DNP ceased quite abruptly after about 1 hr., when the total CO_2 produced amounted to some 4 $\mu\text{l.}/\text{mg.}$ wet wt. of yeast; the initial $Q_{\text{CO}_2}^{\text{N}_2}$ was

about +12. This has been confirmed for the yeast used in the present experiments, in which the initial $Q_{\text{CO}_2}^{\text{N}_2}$ averaged +15 and the CO_2 production anaerobically almost ceased after 1 hr., when 2.5–3 $\mu\text{l.}/\text{mg.}$ wet wt. of yeast had appeared. Aerobically the CO_2 production, although it slowed down, did not stop after 1 hr., but was still proceeding at that point at at least one-half of its initial rate, and was on some occasions reduced to one-half only after 2 hr. The result of this better maintenance of the aerobic-fermentation rate can be seen in Table 8.

Effect of arsenate. In a later paper (Stickland, 1956b) it will be shown that arsenate at $5 \times 10^{-5}\text{M}$ or less inhibits glucose oxidation by yeast by some 80%, but that higher concentrations up to 10^{-3}M are not much more inhibitory, i.e. there is a residuum of arsenate-stable respiration. In the present paper (Table 4) it appears that arsenate, even at 10^{-2}M , scarcely inhibits the endogenous respiration of the same yeast. The arsenate-stable portion of the respiration is of the same order of magnitude in the two cases (Table 9), so it seems possible that the action of arsenate is to suppress glucose oxidation and leave the endogenous respiration intact. If this were so, the R.Q. in presence of glucose and arsenate should be about 0.85, and this has been confirmed by experiment (Table 10).

A further effect of arsenate may be seen in its action in inducing a fermentation of stored polysaccharide, an action similar to that of DNP, except that the effect is marked only with 'enriched' yeast (arsenate 10^{-3}M , 'normal' yeast $Q_{\text{CO}_2}^{\text{O}_2} = +0.7$, 'enriched' yeast $Q_{\text{CO}_2}^{\text{O}_2} = +8$).

Table 7. *Absence of inhibition by iodoacetate of endogenous fermentation induced by DNP*

In each manometer vessel there was 1.0 ml. of suspension of enriched yeast.

Additions	O_2 consumed ($\mu\text{l.}$)	Non- respiratory CO_2 produced ($\mu\text{l.}$)	Polysaccharide equivalent of $\text{O}_2 + \text{CO}_2$ (mg.)	Polysaccharide found (mg.)		
				Initial	Final	Change
None	–961	0	1.29	16.8	16.8	0
DNP 3 mM	–886	+492	3.17	16.8	13.9	–2.9
DNP 3 mM + iodoacetate mM	–886	+514	3.26	16.8	13.7	–3.1

Table 8. *Anaerobic fermentation of polysaccharide induced in yeast by DNP*

In each manometer vessel there was 1.0 ml. of suspension of enriched yeast.

Concn. of DNP (mM)	Gas phase	O_2 consumed ($\mu\text{l.}$)	Non- respiratory CO_2 produced ($\mu\text{l.}$)	Polysaccharide equivalent of			Polysaccharide found (mg.)		
				O_2 (mg.)	CO_2 (mg.)	$\text{O}_2 + \text{CO}_2$ (mg.)	Initial	Final	Change
0	Air	1236	0	1.66	0	1.66	22.0	22.1	+0.1
3	Air	725	564	0.97	2.27	3.24	22.0	19.0	–3.0
0	N_2	0	71*	0	0.28	0.28	22.0	22.0	0.0
3	N_2	0	410	0	1.65	1.65	22.0	20.3	–1.7

* This sample of yeast had an unusually high rate of endogenous fermentation ($Q_{\text{CO}_2}^{\text{N}_2} = +1.4$).

Table 9. *Magnitude of arsenate-stable respiration in yeast in various nutritional states*

State of yeast	Q_{O_2}		Inhibition (%)
	Control	Arsenate (mm)	
Impoverished	-4.3	-3.9	10
Normal	-7.4	-6.0	19
Enriched	-21	-7.3	65
Normal + glucose	-77	-11.9	85

Table 10. *Respiratory quotient of arsenate-stable respiration of yeast in presence of glucose*

The fermentation caused by the inhibition of respiration by arsenate was inhibited by iodoacetate. Each manometer vessel contained 1.0 ml. of 5% yeast suspension (about 14 mg. dry wt.), 0.5 ml. of 0.8% glucose, 0.5 ml. of 0.1M tris, pH 6.5, 0.5 ml. of 6 mM sodium arsenate and 0.5 ml. of 6 mM iodoacetate. Duplicate pairs were set up with and without KOH to absorb the respiratory CO_2 .

State of yeast	R.Q. in glucose + arsenate	R.Q. of endogenous respiration
	+ iodoacetate	
Impoverished	0.85	0.86
Normal	0.89	0.87
Normal	0.78	0.87

DISCUSSION

It is clear from the results presented that the substrate for the respiration when no external oxidizable material is present is, in ordinary commercial baker's yeast, not of carbohydrate nature. This agrees with earlier workers' measurements of R.Q. and is consistent with the fact that no fermentation of stored carbohydrate takes place. The effect of DNP is to make the stored carbohydrate available for breakdown, and this takes place by both

oxidation and fermentation, the oxidation of the non-carbohydrate substrate being suppressed. The nature of the non-carbohydrate material remains unknown; its amount in the yeast cell is reduced by aeration, and increased by treatment of the cell with glucose; the R.Q. of its oxidation is 0.85.

SUMMARY

1. When baker's yeast respires without added substrate its respiratory quotient is 0.85.
2. No stored polysaccharide disappears during this respiration.
3. The respiration is associated with an esterification of inorganic phosphate ($Q_P^0 = -40$).
4. In the presence of 2:4-dinitrophenol (DNP) aerobically a fermentation of stored carbohydrate is set up and the respiration is changed to an oxidation of carbohydrate.
5. The fermentation induced by DNP is not inhibited by $10^{-3}M$ iodoacetate.

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The Pasteur Effect in Normal Yeast and its Inhibition by Various Agents

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As Dickens (1951) has most recently pointed out, no theory yet put forward to explain the Pasteur effect can be considered to exclude numerous other possible theories. The present paper seeks to define the problem more closely as it occurs in yeast, and to dispose of at least one of the conflicting theories that have been proposed to explain the phenomenon.

The definition of the Pasteur effect is commonly stated in two parts: (1) the partial or complete suppression by oxygen of the formation of the products of anaerobic carbohydrate breakdown, and (2) the diminution by oxygen of the rate of carbohydrate breakdown. The first part of the definition may be given quantitative expression by means of