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Effects of O_2 Concentration on Rice Seedlings[1]

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ABSTRACT

The ability of rice, wheat, and oat seedlings to germinate and grow as the O_2 concentration was lowered to zero was compared. The germination of rice was completely unaffected by O_2 supply, whereas that of oats and wheat was strongly retarded at levels below 5% O_2. In contrast to the coleoptiles of oats and wheat and to roots of all three species where growth was progressively diminished as the O_2 concentration was lowered, that of the rice coleoptile was progressively increased. However, the dry weight and content of protein, sugars, and cellulose were all depressed in the rice coleoptile in anoxia, and the levels of several respiratory enzymes, particularly those of mitochondria, were also much lower than those of the coleoptiles grown in air. In 1% O_2, the growth of the rice coleoptile was similar to that in air. The effect of ethanol concentration on germination and growth of rice was measured. Coleoptile growth was reduced when the ethanol concentration exceeded 40 millimolarity, and root growth was somewhat more sensitive. Coleoptiles of all three species grown in air were transferred to N_2, and ethanol accumulation was measured over 24 hours. The rate of ethanol accumulation in oats was close to that in rice, and in all three species the amounts of ethanol lost to the surrounding medium were those expected from simple diffusion from the tissue. The ability of the rice coleoptile to grow in anoxia is apparently not due to a particularly low rate of ethanol formation or to unusual ethanol tolerance. Any explanation of the success of rice in anoxia must encompass the much lower rate of ATP synthesis than that in air and account for the biochemical deficiencies of the coleoptile.

When deprived of O_2, the seeds of most higher plant species fail to germinate, and for plants growing in air the imposition of anaerobic conditions prevents their further growth. Rice is one of the few species whose seeds can germinate in anaerobic conditions. Although there is now an extensive literature on some aspects of growth and anaerobic metabolism in rice, the biochemical basis for its unusual adaptation to anoxia is not known (8). It is frequently inferred that rice germinates better in the absence of O_2, although several authors have emphasized that only the coleoptile elongates and no roots are produced under these conditions (4, 11, 17, 22, 31, 33, 34). In this paper, we present data on the growth and some biochemical features of rice seeds exposed to different levels of O_2 and compare the pattern to that observed in other graminaceous seeds.

MATERIALS AND METHODS

Plant Materials. Rice seeds (*Oryza sativa* cv S-6) were kindly supplied by Dr. D. K. Seaman, University of California Rice Experiment Station, Biggs, California. Wheat seeds (*Triticum sativum* cv MEC) and oat seeds (*Avena sativa* line 912) were provided by The Institute of Agronomy, University of Pisa.

Seeds sterilized in 1% NaOCl were germinated in darkness in 250-ml flasks containing five Whatman No. 1 filter papers and 7 ml H_2O. A moistened gas stream of air, 5% O_2, 1% O_2 or N_2 (99.998% purity) was passed through the flasks at 3 ml/min throughout the experiment period.

Growth Measurements. Increases in fresh and dry weights of roots, coleoptiles, and primary leaves were recorded over a 7-d period.

Effect of Ethanol on Germination. Seeds were germinated in air in darkness in the presence of a graded series of ethanol concentrations from 0.08% (14 mM) to 2% (347 mM). Root and shoot lengths were measured after 5 d.

Analytical Procedures and Enzyme Assays. Total protein content was determined by the Lowry procedure (19). Sucrose was assayed as described (21), and glucose was assayed by the Statzyme method using reagents from Worthington Diagnostics, Freehold, NJ, on extracts prepared as in (14). α-Cellulose was assayed on cell wall preparations (36); wall fractionation and α-amylase treatment to remove starch were performed according to (3). Ethanol extracted from the tissues (16) and that in the surrounding medium was analyzed as described (5). For determinations of enzyme activity, coleoptiles were ground in cold 100 mM Tris·HCl (pH 7.4) and the extract centrifuged at 270*g* for 20 min. The supernatant solution was used for enzyme assays as described; ethanol dehydrogenase (25), catalase (1), Cyt *c* oxidase (12), fumarase (24), phosphofructokinase (28), and triose-P-isomerase (23).

O_2 uptake was measured at 20°C with an O_2 electrode (9). The seeds or seedlings were introduced into the electrode well containing 2.5 ml Mes-Tris buffer (pH 6.1).

RESULTS

Effects of O_2 on Growth and Germination. The response of wheat and rice growth to different O_2 concentrations is shown in Figure 1. Lowering the O_2 concentration to 5% led to decreased growth of both roots and shoots in wheat. In 1% O_2, only two-thirds of the seeds germinated, and the growth rate of roots and shoots of the surviving seedlings was reduced by roughly 50%. In rice, there was some reduction of root growth on lowering the O_2 concentration, but the growth of shoots was increased, as noted by earlier investigators (4, 30, 33).

The ability of rice, wheat, and oats to germinate at different O_2 levels is shown in Table I. No germination of wheat or oats occurred in N_2. At 1% O_2, only 5% of the oat seeds had germinated at 6 d. Germination of both oats and wheat was delayed in 5% O_2 but reached control levels by 6 d. In rice, on the contrary, there was no influence of O_2 level on the rate or percentage of germination. However, as noted previously (17, 32–34), no root growth occurred in N_2 and the growth of the primary leaf was barely detectable even after 2 weeks in anoxia.

Features of the growth of the rice coleoptile in air and N_2 are presented in Figure 2. As shown, the coleoptiles in N_2 grow at a

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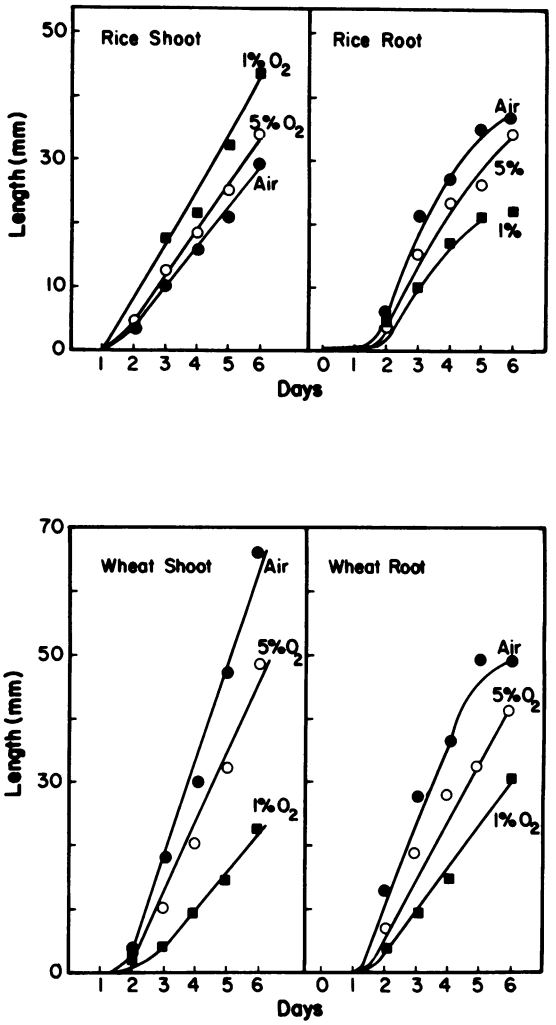

FIG. 1. Growth responses of rice and wheat seedlings at different O_2 concentrations. Note that lowering the O_2 concentration to 1% led to progressive curtailment of growth in shoots and roots of wheat and in rice roots, while growth in length of rice shoots was progressively increased.

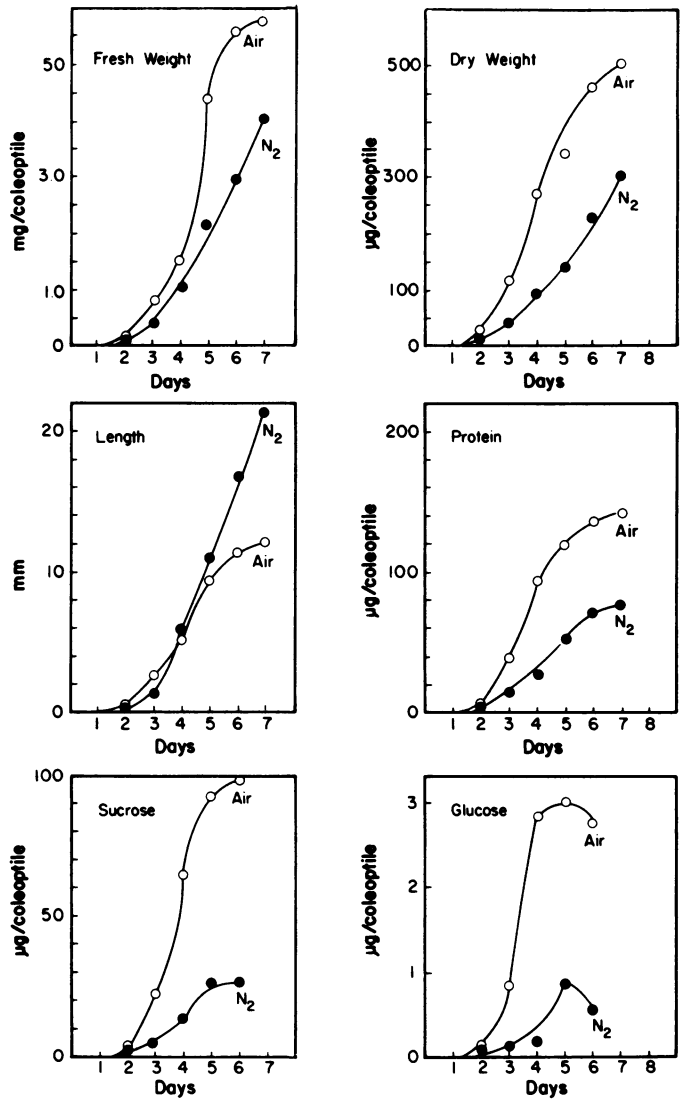

FIG. 2. Changes in fresh weight, dry weight, length, protein, and sugars in rice coleoptiles growing in air and N_2.

Table I. *Germination of Rice, Wheat, and Oats at Different Levels of O_2*

	Day 2	Day 3	Day 4	Day 5	Day 6
			%		
Rice					
Air	79	83	89	90	90
5% O_2	77	83	88	91	92
1% O_2	74	77	78	80	86
N_2	75	78	78	80	82
Wheat					
Air	72	83	88	88	88
5% O_2	28	64	80	84	84
1% O_2	16	56	56	56	56
N_2	0	0	0	0	0
Oats					
Air	77	82	82	89	92
5% O_2	20	56	76	85	84
1% O_2	0	0	2	2	5
N_2	0	0	0	0	0

steady rate between days 3 and 7 and considerably exceeded the length achieved in air. They continue to grow for at least a further week in N_2, whereas the growth of the coleoptile in air ceases at about day 7 (not shown). However, the anaerobic coleoptile is quite thin and fragile and despite its greater length, its fresh weight is less than that in air. During the first 5 d, its dry weight is less than half that of the coleoptiles from seedlings grown in air (Fig. 2). The total protein content of the coleoptile in N_2 is similarly reduced, and the contents of sucrose and glucose are reduced to an even greater degree. In 7-d anaerobic coleoptiles, the α-cellulose content was only 20% of that of coleoptiles from aerobic seedlings.

Thus, although the coleoptiles of rice seedlings grown in N_2 achieve a greater length than those in air, they are inferior in several respects. However, the provision of even a low level of O_2 corrects these deficiencies (Fig. 3). Shoot growth (including coleoptile and first leaf) and protein content in 1% O_2 are similar to those in 5% O_2. One percent O_2 also allows the growth of roots, but at a reduced level compared to that of seedlings in 5% O_2.

Respiration and Enzyme Content of Rice in Anoxia. When coleoptiles from seedlings grown anaerobically for 4 to 6 d were transferred to air and their O_2 uptake measured within 30 min, the results shown in Table II were obtained. At day 4, the O_2 uptake of anaerobically grown coleoptiles was roughly one-sixth of the aerobic controls, and by day 6 this level had increased to one-half. These results are in contrast to those of Vartapetian *et al.* (34) who found that the intensity of respiration remained unchanged in anaerobically grown coleoptiles between days 3 and 7. Nevertheless, mitochondria are present in anaerobically grown

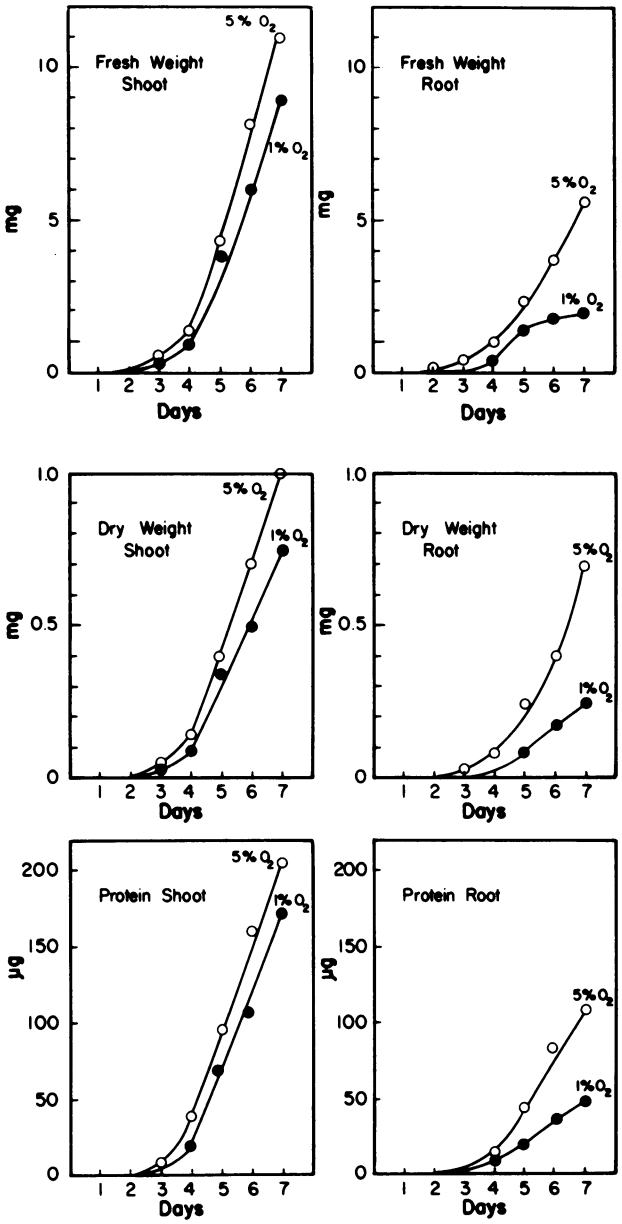

FIG. 3. Growth and protein content of rice coleoptiles and roots in 5% O_2 and 1% O_2. The fresh weight, dry weight, and protein content of shoots are similar in 1% and 5% O_2, whereas in roots these values remained depressed in 1% O_2.

Table II. *Respiration of Rice Coleoptiles Grown in Air and N_2*

Age	Coleoptiles Grown in Air	Coleoptiles Grown in N_2 Transferred to Air for		
		15 min	3 h	24 h
d	*nmol O_2/coleoptile in 10 min*			
4	13.9	2.4		
5	14.8	5.8	9.1	15.8
6	15.3	8.2		

coleoptiles and these have been intensively examined by Vartapetian (35). In discussing these and his own results, Tsuji (33) has argued convincingly that some capacity for aerobic respiration, and the mitochondria which implement it, develop under anaerobic conditions, but that this is not sustained during development. However, when anaerobically grown coleoptiles were exposed to air for a period of several hours, Tsuji (33) showed that there was a rapid increase in O_2 uptake to the levels of aerobically grown coleoptiles in 12 h. A similar result for the 5-d coleoptiles grown in our conditions is shown in Table II. Vartapetian *et al.* (35) showed that after transfer to air there was an increase in the level of Cyt *c* oxidase, measured histochemically. Our results confirm this result qualitatively, but recovery was not complete. Thus, after transfer of coleoptiles from 5-d seedlings to air, the Cyt *c* oxidase, with an initial activity of 3.1 nmol/min·coleoptile, increased to 5.7 nmol/min at 3 h and 14.8 at 24 h, whereas the 6-d aerobically grown coleoptile showed a value of 28.2 nmol/min.

The levels of other enzymes in coleoptiles from anaerobic and aerobic conditions are shown in Table III. Except for alcohol dehydrogenase, all of the enzymes assayed were present at lower levels in the anaerobic coleoptiles. However, the mitochondrial enzymes fumarase and Cyt *c* oxidase were much more strongly depressed in anaerobic conditions than the glycolytic enzymes phosphofructokinase and triose-P-isomerase. Catalase activity was reduced by more than 90% in anaerobic rice coleoptiles (Table III), and a similar effect was shown in wheat and oat. Even at 5% O_2, catalase activity in all three species was less than 50% of that in aerobic conditions.

As noted by many previous authors, alcohol dehydrogenase activity increased in anoxia to levels considerably exceeding those in air (2, 4, 8, 15). Although Crawford (7) has argued that high rates of ethanol production and increased levels of alcohol dehydrogenase are characteristic of species intolerant of anoxia, this has been questioned previously, *e.g.* by Davies (8) and Avadhani *et al.* (4). The levels of alcohol dehydrogenase even under aerobic conditions are more than adequate to account for the rates of ethanol formation observed in anoxia, and the significance of the anaerobic rise in the activity of this enzyme is not at all clear. The picture is further complicated by the observation that a specific endogenous inhibitor (inactivator) of ethanol dehydrogenase is present in some species (13).

Ethanol Accumulation and Toxicity. It is frequently inferred that the adverse effects of anoxia are due to the accumulating ethanol. However, as Drew (10) has argued, the concentrations of ethanol required for the inhibition of growth (30–170 mM) are rarely approached even in long-term experimental or in natural waterlogged conditions, and the effects of anoxia on growth are frequently immediate.

The effects of ethanol on rice germination are shown in Table IV. Even at concentrations greater than 300 mM, some coleoptile elongation was observed and roots were produced at concentrations less than 50 mM. Subsequent growth of coleoptiles and roots was noticeably reduced only when the ethanol concentration in the medium exceeded 40 mM. An important ameliorating feature of the possible toxic effects of accumulating ethanol which has been recognized by some authors (*e.g.* 6, 27, 29) is the escape of ethanol to the surrounding medium. Clearly, unless the ethanol is actively retained against its concentration gradient, the amount accumulating in the tissue will depend on the volume of the surrounding medium (and, under natural conditions of waterlogging, on the ability of microorganisms to decompose it). Curiously, although the amounts of ethanol in tissue and surrounding medium have frequently been measured, it has not been shown whether the leakage is a purely diffusive process.

The results (Table V) establish that the ethanol produced by submerged coleoptiles of all three species reaches the equilibrium expected from diffusion within 12 h of the imposition of anoxia. The amounts of ethanol in the tissue and bathing solutions are in proportion to their volumes, showing that the total ethanol concentration in the water space of the tissue is close to that in the external solution at 12 h. The results (Table V) also show that the rate of ethanol accumulation in oat coleoptiles, which are intol-

Table III. *Enzyme Activity of Extracts from Rice Coleoptiles from Seedlings Grown in Air or N_2*

Enzyme	Day 4		Day 5		Day 6	
	Air	N_2	Air	N_2	Air	N
	nmol/coleoptile·min					
Phosphofructokinase	0.675	0.128	0.698	0.470	1.125	0.910
Triose-P-isomerase	280	126	295	342	430	271
Fumarase	0.044	0.038	0.200	0.087	0.388	0.077
Cyt *c* oxidase	9.8	1.4	17.3	2.3	28.0	2.9
Alcohol dehydrogenase	44,100	38,200	50,500	85,000	83,200	149,000
Catalase	29,200	2,060	84,400	6,450	178,200	12,400

Table IV. *Effect of Ethanol on Rice Germination*

Seeds were incubated in air for 5 d under the standard conditions with ethanol as indicated.

Ethanol Concn.		Root Length	Coleoptile Length
%	mM	*mm*	
2	347	No root	1
1	174	No root	1.5
0.5	87	1.7	2.6
0.25	43	2.2	3.0
0.12	21	3.5	4.2
0.08	14	3.9	4.9
0	0	4.1	4.7

Table V. *Ethanol Accumulation in Coleoptiles and Medium*

Coleoptiles (300 mg) were submerged in 1 ml 5 mM Mes-Tris buffer (pH 6.1) containing 0.5 mM $CaCl_2$, 1 mM KCl in 1.5-ml vials with serum stoppers. The vials were gassed with N_2 and duplicate vials sampled at the times indicated. The amounts of ethanol in the tissue (volume, ~0.3 ml) and solution (volume, 1 ml) were determined.

	Incubation Time (h)			
	3	6	12	24
Rice				
Ethanol in tissue, μmol	5.8	9.3	10.4	13.4
Ethanol in medium, μmol	12.2	18.3	38.1	50.4
Total ethanol, μmol	18.0	27.6	48.5	63.8
Volume of tissue, % of total	23	23	23	23
% of ethanol in tissue	31	29	21	21
Wheat				
Ethanol in tissue, μmol	2.2	3.6	5.0	5.0
Ethanol in medium, μmol	3.5	7.0	17.0	28.0
Total ethanol, μmol	5.7	10.6	22.0	33.0
Volume of tissue, % of total	23	23	23	23
% of ethanol in tissue	39	34	23	15
Oat				
Ethanol in tissue, μmol	5.3	5.6	9.0	12.5
Ethanol in medium, μmol	7.0	10.0	33.0	50.0
Total ethanol, μmol	12.3	15.6	42.0	62.5
Volume of tissue, % of total	23	23	23	23
% of ethanol in tissue	43	36	22	20

erant of anoxia, is almost as great as that in rice coleoptiles which can grow under these conditions.

DISCUSSION

The present results, while confirming the unusual ability of the rice coleoptile to grow under anaerobic conditions, emphasize that the growth is far from normal. With respect to dry weight, protein content, cellulose and sugar content, and various enzyme activities, the resulting coleoptile is markedly deficient compared to coleoptiles in air, and it is known that in rice (22) and in the comparable oryzicola (27) cell division is very restricted. Only in respect to length is the coleoptile grown in low O_2 superior. Many previous authors have emphasized this aspect and recognized that the greater length achieved in low O_2 may be of distinct advantage in allowing access to regions less deficient in O_2 when it is growing under water. However, somewhat different quantitative responses to low O_2 have been recorded. Tsuji, in a comprehensive and perceptive review (33), cites his own and other results (4, 26) which show that maximum growth in length was achieved at some low O_2 concentrations above zero, and suggests that limitation of the normal aerobic breakdown of auxin may be the cause. Under our conditions, the growth in length of the coleoptile was progressively increased as the concentration of O_2 was reduced to zero (Fig. 2). It is not clear whether this difference in response is due to the way in which treatment was carried out, to possible influences of ethylene (18), or whether it is due to varietal differences.

The results show that the ability of the rice coleoptile to grow anaerobically is not due to an unusually low production of ethanol and, as has been repeatedly observed (4, 14), alcohol dehydrogenase activity increases in anoxia as it does in many plants whose growth is markedly sensitive to low O_2. As Drew (10) has emphasized, and as shown here, the effects of low O_2 on growth are exerted long before the accumulating ethanol reaches toxic levels, and it is widely recognized (4, 6, 27, 29) that ethanol passes out of the tissue into the surrounding medium, which we now show occurs in accordance with simple diffusion (Table V). And in any event, the rice coleoptile does not appear to be peculiarly resistant to ethanol (27).

How then is the unusual ability of rice (and of the riceweed oryzicola [27]) to produce an actively elongating coleoptile in N_2 to be explained? It appears that no significant amounts of anaerobic products other than ethanol are produced (4), and appropriately, attention has focused on the ability to exploit the substrate level phosphorylations that occur in glycolysis (33). Of course, ATP production in anaerobiosis is perhaps one fifteenth of that in air for a given amount of glucose. Thus, only if the rate of glycolysis in anoxia was 15-fold that in air would an equivalent amount of ATP be generated, and although a pronounced Pasteur effect has been recorded for rice (30) though not for oryzicola (27), there is no suggestion that the rate is increased so far as to remotely approach the rate of ATP generation in air.

In a continuing investigation of this problem, Pradet has shown (20 and references therein) that, in contrast to other plant tissues, the energy charge in the coleoptile recovers to a fairly high value (0.80) after the usual decline on transfer to anaerobic conditions. They showed that the rate of anaerobic incorporation of amino acids into protein was correlated with the changes in energy charge and suggest that the maintenance of the high energy charge may account for the success of rice in anoxia (20).

However, for the reasons given above, it is most unlikely that the amount of ATP generated in anoxia (and thus presumably the rate of synthetic events) is close to that in air. Indeed, although some incorporation of amino acid into protein did occur in anaerobic conditions, it is clear that net protein synthesis was

abolished in Pradet's experiments (20). Some new proteins appeared in anaerobiosis, and the suggestion was made that these may "allow a more efficient anoxic metabolism" (20). Evidence is awaited for such a mechanism; meanwhile, the enigma remains.

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