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The Mechanism of Ethylene and Cyanide Action in Triggering the Rise in Respiration in Potato Tubers[1]

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ABSTRACT

Ethylene and cyanide induce a sharp increase in respiration in potato tubers (*Solanum tuberosum*, var. Russet) attended by changes in the glycolytic intermediates which indicate that both gases enhance glycolysis. The level of sucrose also increases in response to both treatments. The data are taken to indicate that both cyanide and ethylene either activate or affect the link between the conventional electron transport chain and the cyanide-insensitive path. It is further proposed that this activation may well be the primary event leading to the rise in respiration. Ethylene increases the level of adenosine 5′-triphosphate and it is suggested that because of the 4- to 6-fold increase in the rate of electron flux through site I, which continues to operate in the over-all cyanide-insensitive path, the absolute levels of adenosine 5′-triphosphate will also be expected to increase in the presence of cyanide. The increase in sucrose content is considered to be the consequence of the rise in adenosine 5′-triphosphate concentration.

Ethylene and cyanide have been shown to elicit similar physiological changes in avocado fruits (23). At the time it was indicated that ethylene and cyanide, in stimulating respiration, may release the same regulatory restraints (although not necessarily by identical means). The effect of ethylene on plant respiration was described as a fundamental process independent of ripening. We have extended our studies of the effects of cyanide and ethylene to the respiration of potato tubers, an organ wherein respiration is stimulated both by ethylene and cyanide (15, 16, 20), and where ripening is not involved.

MATERIALS AND METHODS

Potato tubers (*Solanum tuberosum*, var. Russet) were grown at Tule Lake, in northern California, and stored at 7 C. Before an experiment, tubers were put in 4-liter respiratory jars through which a stream of air or appropriate mixture of air and experimental gas was passed over the tubers at 50 ml/min. The rates of CO_2 output and O_2 uptake were determined with a Beckman infrared CO_2 analyzer and oxygen analyzer, respectively.

Phosphate esters and lactate were extracted and purified as described earlier (23), omitting charcoal purification in the case of ATP determination. They were determined enzymatically in systems linked to spectrophotometric measurements of changes in NADH levels (9). In the determination of simple sugars, the tissue was first homogenized in 10% cold perchloric acid and centrifuged, and the residue was twice extracted with 5% perchlorate and centrifuged. The three supernatants were combined, and the pH was adjusted to 7 with KOH. The extract was subsequently left overnight at 3 C. Potassium perchlorate was removed by centrifugation, and the supernatant solution was evaporated to about 5 ml with a rotary evaporator at 35 C. The extract was taken up to a convenient volume with distilled H_2O. Sugars were determined enzymatically according to previously published methods (9). α-Keto acids were determined by the method of Isherwood and Niavis (18). Tissue slices cut from each tuber were dropped into liquid nitrogen and ground therein. Thirty g of powder were weighed as quickly as possible, and homogenized with a high speed blender in a mixture of 0.6 M metaphosphoric acid, 60% methanol, and Dry Ice, at −60 C. The subsequent procedure followed that of Isherwood and Niavis (18). The phenylhydrazones of the α-keto acids were separated by paper chromatography on a single paper buffered with 0.1 M phosphate, pH 6.2, and developed with tertiary amyl alcohol-water (80:20 v/v). Cyanide and ethylene gases were applied as described previously (23).

RESULTS

Ethylene Effects on Respiratory Activity of Potato Tubers. Figure 1, a and b, shows the courses of O_2 uptake and CO_2 output of tubers subjected to 30 μl/l of ethylene. Within about 5 hr, ethylene induces a rapid increase in the rate of respiration, which reaches a peak in about 20 to 22 hr, falls off rapidly in the next few hours, and declines more slowly thereafter. The level of respiration after the peak varies with the experiment. In Figure 1a, for example, the rate of respiration after the initial postpeak decline remains elevated for 150 hr, whereas in Figure 1b the respiration declines to almost the control level within 40 hr. Postpeak respiration rates depend on the batch of potatoes. Similar observations have been reported previously (20). Another characteristic of the initial sharp rise in respiration is the low RQ values which, in the interval of 8 to 18 hr after treatment, can be as low as 0.3. It is not clear whether the low value is the result of the difference in solubility of O_2

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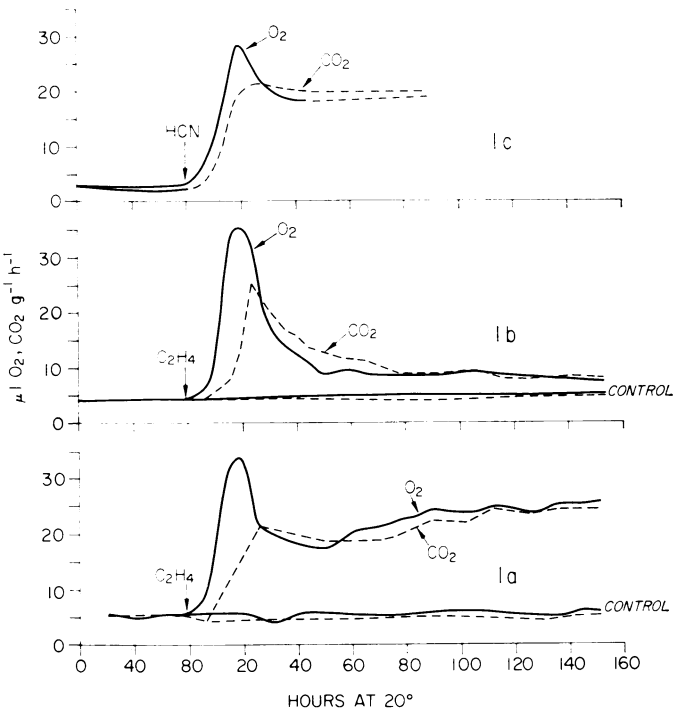

FIG. 1 a and b: Effect of 30 μl/l of ethylene on the rates of O_2 uptake and CO_2 output of potato tubers; c: effect of 650 μl/l HCN on the rates of O_2 uptake and CO_2 output on potato tubers. O_2 uptake (——); CO_2 output (– – –).

Table I. *Effect of Ethylene on Rates of Respiration and Concentration of Glycolytic Intermediates in Potato Tubers*

Treatment and Sample No.	Respiration Rate	Glycolytic Intermediates			
		FDP	TP	G6P	PEP
	$\mu l\ O_2/g \cdot hr$	*nmoles/g fresh wt*			
Control					
1	3	~0.05	0.09	135	65
2	2.8	~0.05	0.08	139	58
3	2.7		0.10	155	70
30 μl/l C_2H_4					
4 (12 hr)	9.6	0.358	2.9	87	28
5 (13 hr)	9.8	0.245	2.6	84	32
6 (14 hr)	9.5	0.321	2.8	93	30
7 (14 hr)	7.3	0.402	3.5	97	27
8 (19 hr)	12.3	0.312	2.5	107	33
9 (18 hr)	13.8	0.208	1.8	108	29

and CO_2, the effects of which would be noted in the period of rapid transition, or whether the low RQ has a bonafide metabolic origin.

Table I indicates the levels of glycolytic intermediates in the interval of 12 to 19 hr after the application of ethylene, during which time the rate of respiration usually increases rapidly. The glycolytic intermediates can be divided into two groups, according to whether their concentration increases or decreases in this period. In the first group belong TP[2] and FDP, whose levels increase sharply. In the second belong PEP, 3-PGA, and G6P, whose concentrations decrease appreciably. A similar pattern of changes has been found with certain climacteric fruits, *viz.* bananas (7, 21), tomatoes (11), and avocados (23). It has also been observed in plant and animal tissues as well as in yeast, when glycolysis is accelerated by anaerobiosis (6, 13, 19).

Effect of Anoxia on Untreated and Ethylene-treated Potato Tubers. Potato tubers show an increase in the rate of carbohydrate breakdown when transferred to N_2, accompanied by changes in the levels of glycolytic intermediates similar to those reported above which occur in response to ethylene (5). To determine the glycolytic capacity of these potato tubers, and to establish a relationship between the rate of glycolysis and the pattern of changes in the glycolytic intermediates, both untreated and ethylene-treated tubers were made anaerobic, and measurements were made of CO_2 evolution, of lactate production, and of the concentrations of glycolytic intermediates and ATP. The rate of CO_2 evolution of tubers treated with ethylene for 22 hr continued to rise for about 4 hr after transition to N_2. Thereafter the rate of CO_2 production fell off slowly and seemed to reach a steady state in about 20 hr (Fig. 2a). CO_2 output of untreated tubers at first decreased slightly after anaerobiosis, then gradually increased (Fig. 2b). The values of CO_2 output quoted in Table II are those observed immediately before extraction. Table II depicts the rate of respiratory carbon utilization for all cases. With aerobic tubers, the rate of CO_2 output was taken as a direct measure of the rate of glucose oxidation, for no lactate or ethanol accumulates in air. The carbon traffic in anaerobic tubers is calculated by assuming that in N_2, CO_2 and ethanol production are equal, and by converting ethanol and lactate to their carbon equivalents. The data show that ethylene increases the rate of carbon utilization in respiration about 3-fold. Tubers treated for 22 hr with ethylene and then made anaerobic show a rate of respiratory carbon utilization which is 7- to 8-fold that of untreated tubers in air. Anoxia alone enhances the rate of carbohydrate breakdown by about 4.5 times. It is apparent that ethylene pretreatment further stimulates glycolysis in N_2. The data show that the glycolytic capacity of the tubers is more than adequate to sustain the rate of respiration in air observed in response to ethylene. Because anaerobiosis in turn further stimulates glycolysis in the presence of ethylene, it follows that glycolytic control is not totally released by ethylene alone. The foregoing deduction is reinforced by the observation that the postpeak respiration rate frequently drops almost to that of untreated tubers, notwithstanding the presence of ethylene (Fig. 1b). Table III sets out the effect of anaerobiosis and ethylene, separately and together, on the levels of some glycolytic intermediates and ATP. Ethylene raises the level of ATP by 7- to 8-fold at the peak of the respiratory activity. The pattern of changes in the glycolytic intermediates in anaerobic and ethylene-treated anaerobic tubers is similar to that shown in Table I for tubers kept in ethylene. Similar changes in PEP and 3-PGA in potato tubers kept in N_2 have been reported previously (5). Anoxia sharply decreases the level of ATP in both ethylene-treated and control tubers. The drop is proportionally larger in the former case, where ATP drops from about 550 nmoles/g fresh weight to approximately 25 nmoles/g fresh weight.

Effect of Ethylene on Sucrose and Glucose Levels. Table IV shows that when respiration remains elevated in response to ethylene from 150 to 160 hr, both sucrose and glucose contents increase sharply.

Cyanide Effects on Respiratory Activity and Intermediates of Potato Tubers. The effect of cyanide on the rate of tuber

[2] Abbreviations: TP: triose phosphate; FDP: fructose 1,6-diphosphate; 3-PGA: 3-phosphoglyceric acid; G6P: glucose 6-phosphate; PEP: phosphoenol pyruvate; PFK: phosphofructokinase; PK: pyruvate kinase.

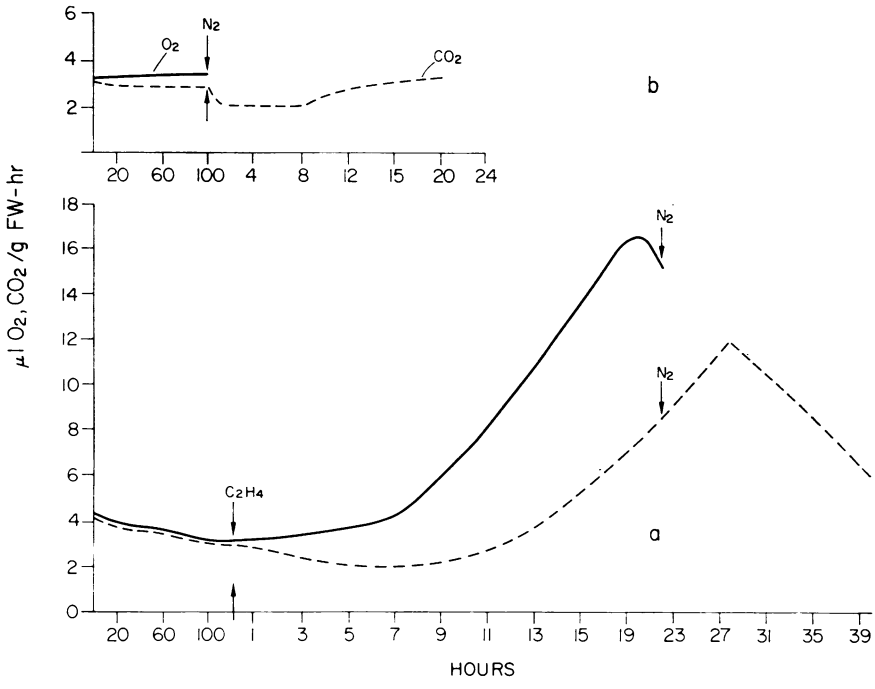

FIG. 2. a: Rate of O_2 uptake and CO_2 output of tubers treated with 30 μl/l of ethylene and then kept in N_2 for a further 20 hr; b: rate of CO output of tubers kept in N_2 for 20 hr. O_2 uptake (——); CO_2 output (– – –).

Table II. *Effect of Ethylene and Anaerobiosis on CO_2 Output, Lactate Production, and Carbon Utilization in Potato Tubers*

Treatment and Sample No.	Respiration Rate	Lactate Production	Respiratory Carbon		Relative Rates of Carbon Utilization (Treated/Control)
	μl CO_2/g fresh wt·hr	nmoles/g fresh wt·hr	nmoles carbon/g fresh wt·hr[1]	total nmoles carbon/g fresh wt·hr[2]	
Control					
1	3		135	135	
2	2.8		125	125	
3	2.8		125	125	
30 μl/l C_2H_4 for 22 hr					
4	7.95		356	356	2.8
5	6.90		306	306	2.6
6	8.10		360	360	2.84
30 μl/l C_2H_4 for 22 hr followed by 20 hr in N_2					
7	6.4	48	860	1000	8.05
8	6.4	70	860	1070	8.03
9	5.5	56.5	735	910	7.04
20 hr in N_2					
10	3.5	42	478	604	4.75
11	3.4	37	455	566	4.46
12	3.3	43	441	570	4.49

[1] This rate is calculated by assuming that in N_2, CO_2 was produced from decarboxylation of pyruvate.

[2] To the above value, the nmoles of carbon due to lactate production are added.

Table III. *Comparative Effect of Ethylene and Anaerobiosis on Rate of CO_2 Evolution and on Concentration of Glycolytic Intermediates, ATP, and Lactate*

Treatment and Sample No.	Rate of CO_2 Evolution	FDP	G6P	3-PGA	ATP	Lactate
	μl/g fresh wt·hr	nmoles/g fresh wt·hr				
Control						
1	3	~0.05	187	95.8	76.8	90
2	2.8	<0.05	170	90.5	77	86
3	2.7	<0.05	169	98	80	
30 μl/l C_2H_4 for 22 hr						
4	7.95	0.302	111	51	615	
5	6.90	0.360	104	61	501	
6	8.10	0.250	118	65	550	
30 μl/l C_2H_4 for 22 hr followed by 20 hr in N_2						
7	6.4	0.134	65	28	20	960
8	6.4	0.118	85	33	28.5	1400
9	5.5		72.5	19	18	1130
20 hr in N_2						
10	3.5	0.279	90.6	25	10	840
11	3.4	0.105	107	23	9.5	640
12	3.3	0.219	106	27.5		860

respiration is depicted in Figure 1c. Cyanide, like ethylene, initiates a sharp rise in respiration rate after 4 to 6 hr, which reaches a peak in 20 hr and thereafter declines. As in the case of ethylene, the final rate of respiration varies with the batch of tubers. Respiration may remain elevated, as in Figure 1c, or may decrease to almost the pretreatment level within 40 to 50 hr. Another similarity between cyanide- and ethylene-stimulated respiration is that the initial RQ values are considerably lower than unity in both cases.

Table V demonstrates the changes in the concentrations of glycolytic intermediates in response to cyanide. The initial cyanide-evoked increase in the rate of respiration is associated with a pattern of changes in the glycolytic intermediates similar, but for G6P, to that found in anaerobic and ethylene-

Table IV. *Respiration Rates and Sucrose and Glucose Levels in Tubers Treated with Ethylene*

Treatment and Sample No.	Respiration Rate	Sugar	
		Sucrose	Glucose
	μl O_2/g fresh wt·hr	*μmoles/g fresh wt*	
Experiment I			
Control			
1	2.3	0.98	1.55
2	2.5	1.30	2.7
30 μl/l C_2H_4			
3 (167 hr)	3.5	2.65	7.4
4 (155 hr)	3.7	3.30	10.1
5 (166 hr)	6	12.2	25.3
6 (154 hr)	9.4	8.9	18.2
Experiment II			
Control			
1	2.3	1.3	3.6
2	2.2	1.4	3.3
3	2.4	1.7	2.8
4	2.5	1.2	3.6
30 μl/l C_2H_4			
5 (162 hr)	4	3.52	8.7
6 (165 hr)	9.5	10.2	26.3
7 (162 hr)	10.8	11.8	30.2
8 (161 hr)	11.4	15.5	34

Table V. *Effect of Cyanide on Respiration Rate and Concentration of Glycolytic Intermediates, α-Keto Acids, and Lactate*

Treatment and Sample No.	Respiration Rate	FDP	G6P	3-PGA	Pyruvate	α-Ketoglutarate	Lactate
	μl O_2/g fresh wt·hr	*nmoles/g fresh wt*					
Experiment I							
Control							
1	3.2		157	105			
2	2.9	0.25	144	109			
3	3	0.46	172	110			
650 μl/l HCN							
4 (18 hr)	14	2.4	158	50			
5 (19 hr)	13.6	2.22	165	77			
6 (19 hr)	14	1.59	114	77.4			
7 (23 hr)	17.5	1.84	132	79.5			
8 (25 hr)	13.6	1.58	135	70			
Experiment II							
Control							
1	3.3				0.75	3.5	160
2	2.9				0.58		172
650 μl/l HCN							
3	15				25.5	35	223
4	14.2				12.1	41.8	222
5	13.5				11.6	28.2	240

treated tubers. Here, as in the latter instances, the most pronounced changes are shown by FDP, whose level rises by about 4- to 6-fold. It is evident that cyanide and ethylene stimulate glycolytic activity of intact potato tubers with very similar consequences.

Table V shows that both pyruvate and α-ketoglutarate increase markedly in response to cyanide treatment. The reciprocal change in concentration of pyruvate and PEP in response to the over-all increase in metabolic flux indicates the activation of PK (12, 13). We have found that 3-PGA and PEP invariably change in parallel. Thus the changes in 3-PGA of Table V are taken to indicate those of PEP as well. The rise in α-ketoglutarate, concomitant with a 4- to 5-fold increase in the rate of respiration, suggests an enhanced flux into the tricarboxylic acid cycle.

As in the case of ethylene, cyanide markedly increases the level of sucrose where the rate of respiration remains at relatively high levels (Table VI). An increase in both respiration and sucrose concentration in potato tubers in response to cyanide has been reported earlier (15).

DISCUSSION

The enhancement by anoxia of glycolysis in potato tubers induces a characteristic pattern of changes in the glycolytic intermediates, which denotes the activation of two regulatory enzymes, *viz.* PFK and PK (1, 12). This general pattern of changes in the glycolytic intermediates has been found to occur in a variety of cells and tissues where glycolysis is activated by anaerobiosis (6, 13, 19). The similarity in the pattern of changes between anaerobic and ethylene-treated tubers suggests that glycolysis is enhanced in the latter. Although the increase in the rate of glycolysis in anoxia can be explained in terms of the decrease in ATP (Table III), the energy charge increases in the presence of ethylene (Table III), assuming a constant total amount of adenine nucleotides. It is evident that glycolytic activity is not regulated by energy charge alone. While ethylene releases glycolysis in the face of an increased energy charge, glycolysis remains responsive to the latter, as exemplified by the enhancement of the rate of carbohydrate utilization when ethylene-treated tubers are made anaerobic, and ATP drops sharply (Table III). The decline in respiration following the ethylene-induced peak follows upon a sharp rise in the level of ATP (Table III), and may well be caused thereby (Table III). This enhancement of glycolysis by ethylene apparently is not the result of *de novo* synthesis of glycolytic enzymes, for the glycolytic capacity of potato tubers, as realized by anaerobiosis, exceeds that in the presence of ethylene (Table II). There are compelling reasons to believe that the enhancement of glycolysis itself does not account for the respiratory stimulation in connection with the natural climacteric or in response to ethylene or cyanide. We are led to the view that ethylene directly enhances both glycolysis and aerobic respiration with a concomitant increase in ATP levels.

For respiration to remain elevated, ATP must be utilized rapidly. ATP can be turned over either by use in anabolic reactions or by direct hydrolysis. A metabolic process which effectively utilizes ATP is the starch-sucrose interconversion. It is known that potato tubers accumulate simple sugars at low temperatures which disappear on return to higher temperatures. In both instances respiration is activated and ATP is utilized

Table VI. *Effect of Cyanide on Sucrose Content*

Treatment and Sample No.	Respiration Rate	Sucrose Content
	μl O_2/g fresh wt·hr	*μmoles/g fresh wt*
Control		
1	4.8	4.2
2	5.2	5.4
650 μl/l HCN		
3 (70 hr)	20.5	9.10
4 (70 hr)	20.6	10.7
5 (70 hr)	21	9.7

(4, 17); thus, sucrose formation can be an effective sink for ATP utilization. Table IV shows that when respiration remains elevated for 150 to 160 hr, there is a large accumulation of sucrose and glucose. The higher the level of respiration, the larger the accumulation of sugars tends to be. These observations suggest that the formation of sucrose may be the consequence of the increase in ATP levels, and presumably in energy charge, in response to ethylene treatment (Table III). We have pointed out elsewhere (22, 23) that ATP increases during the climacteric in several fruits. It may therefore be argued that certain climacteric-related anabolic activities are the result of heightened energy charge, and that the nature of these anabolic reactions will depend on the fruit in question. Ethylene seems to decontrol respiration with a concomitant increase in ATP levels, which in turn leads to further biochemical changes which depend on the tissue under consideration.

Cyanide, as an inhibitor of Cyt oxidase, would be expected to simulate anaerobiosis and thus enhance glycolysis. The pattern of changes in glycolytic intermediates in response to cyanide indicates that cyanide indeed enhances glycolysis (Table V). The existence of a cyanide-resistant electron path, however, provides for the complete oxidation of pyruvate with no accumulation of glycolytic end products unless the rate of glycolysis exceeds the oxidative capacity of the alternate path. The present data show no lactate accumulation (Table V) and an RQ lower than, or close to unity (Fig. 1c). Thus, in the case of potato tubers in cyanide, the oxidative activity of the alternate path keeps pace with glycolysis. It has been pointed out that the sharp fall in respiration which follows the respiratory peak induced by ethylene may be the result of the increase in ATP. The fact that cyanide-stimulated respiration behaves identically to ethylene-evoked respiration suggests that ATP may rise in the presence of cyanide.

Bendall and Bonner (8) have shown that the alternate path branches from the respiratory chain at the flavoprotein level on the substrate side of Cyt *b*. Although the alternate path *per se* is not coupled to phosphorylation (3), over-all electron transport includes phosphorylation at site I (2, 3). Because in contrast to potato tubers, isolated potato mitochondria are strongly cyanide sensitive, we have been unable to verify the foregoing presumption directly in potato. However, we have investigated a variety of tissues which are stimulated by both ethylene and cyanide, and from among them have isolated mitochondria which on the one hand are cyanide insensitive, and on the other, in the presence of cyanide with malate as substrate, show an ADP/O ratio of 0.7 and a respiratory control ratio of 2.5 (unpublished data). Hence the 4- to 6-fold respiratory increase in response to cyanide in potato tubers may result in an appreciable increase in ATP, as is the case with ethylene (Table III)—because of the enhanced rate of electron transport through site I and the increase in substrate level phosphorylation—at the same time that phosphorylative efficiency is curtailed. Although cyanide initially decontrols (hence, stimulates) both glycolysis and aerobic respiration, the build-up of ATP may subsequently diminish the glycolytic flux, as suggested earlier for ethylene. As noted, sucrose formation can be considered an efficient sink for ATP utilization. The data of Table VI, as well as those of Hanes and Barker (15), indicate that a sustained increase in the rate of respiration by cyanide is associated with an increase in the level of sucrose in potato tubers.

The stimulation of respiration by cyanide is linked to the operation of the alternate path. In light of the similarities between the actions of ethylene and cyanide on potato tubers, it is reasonable to assume that the enhancement of respiration in potato tubers by ethylene is also linked to the operation of the alternate path. We have recently established that in a variety of tissues the presence of the alternate path is a prerequisite for ethylene stimulation of plant respiration (24).

Bahr and Bonner (3) have suggested that cyanide effects the diversion of electrons to the alternate path by dint of Cyt oxidase inhibition, and a mechanism has been proposed to explain the apportioning of respiratory electrons between the two paths. According to this view, a restriction of electron flow through Cyt oxidase implements the alternate path. Although the above proposition can account for cyanide resistance, it cannot account for the action of ethylene, for the latter is not an inhibitor of Cyt oxidase. More to the point, it cannot account for the stimulation of respiration by both cyanide and ethylene. It must be recognized that *in vivo* both Cyt oxidase and the alternate path are greatly restricted. In the presence of uncouplers, the respiration of fresh potato slices is 15 to 30 times that of intact tubers, and 70% is cyanide sensitive (14). In intact tubers, therefore, only a small fraction of the Cyt oxidase capacity is realized, even if it is assumed that all respiration is mediated *via* Cyt oxidase. The fact that HCN evokes a 4- to 6-fold increase in the rate of tuber respiration suggests that the cyanide-resistant path is in limited, if any, use in untreated tubers. If both pathways are used at full capacity, the inhibition of either will result in a drop in respiration. Enhancement of respiratory activity by cyanide can occur if the rate of respiration before treatment is lower than the capacity of the alternate path in the presence of cyanide, At the same time, cyanide and ethylene must engage the alternate path. A mere diversion of electrons from the Cyt oxidase to the alternate path will prevent diminution of respiration but it will not increase it. The effect of ethylene and cyanide on respiration must be directly related to the engagement of the cyanide-resistant path and independent of the simultaneous inhibition of Cyt oxidase. In this connection we have found that CO at concentrations not expected to inhibit Cyt oxidase (less than 1%) enhances the rate of respiration of intact tubers in a manner similar to that of ethylene and cyanide (unpublished data). Consequently, we feel that ethylene and cyanide must either alter the characteristics of the alternate path, so that electron transport is selectively favored therein, or facilitate the bridge to the alternate path. Certain lines of evidence indicate that changes in the physical characteristics of cellular membranes (in this case mitochondrial membranes) may implement the alternate path. Thus, agents which, *inter alia,* can affect the physical characteristics of cellular membranes, induce the climacteric rise in respiration in avocados and bananas (22). Furthermore, it appears that the bridge to the alternate path may be tenuous, for both isolated potato and avocado mitochondria are totally inhibited by cyanide, whereas the respective intact tissues are stimulated by cyanide (2, 10, 23). The process of isolating mitochondria seemingly eliminates the alternate path.

In view of the above discussion, it will be expected that once the activation or the linking of the alternate path has been realized, the maximal flow of electrons will be dependent upon the intrinsic capacity of the alternate path, ADP regeneration at site I, and substrate availability, or a combination of these factors.

Ethylene and possibly cyanide enhance respiration in the presence of high levels of ATP. It seems, therefore, that phosphorylative sites II and III of the conventional electron transport chain are markedly more rate-restricting than site I, for unimpaired function of site I in the presence of ethylene and cyanide allows high rates of respiration in the face of increased levels of ATP. The circumvention of the last two phosphorylating sites seems to have profound physiological consequences. Not only are aerobic respiration and glycolysis

decontrolled and thus activated, despite the rise in ATP levels, but the metabolism of carbohydrates is affected, as evidenced by the extensive formation of simple sugars from starch (17). Both ethylene and cyanide induce identical physiological and biochemical changes in potato tubers, where ripening is not at issue, and in climacteric avocado tissues (23). The similarity of action of the two gases indicates that they trigger the rise by similarly affecting parameters involved in the regulation of both aerobic respiration and glycolysis. In this view, the activation of the alternate path may well be the primary event leading to the increase in respiration.

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