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Effect of Silver Ion, Carbon Dioxide, and Oxygen on Ethylene Action and Metabolism[1]

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ABSTRACT

The relationship between ethylene action and metabolism was investigated in the etiolated pea seedling (*Pisum sativum* L. cv. Alaska) by inhibiting ethylene action with Ag^+, high CO_2, and low O_2 and then determining if ethylene metabolism was inhibited in a similar manner. Ag^+ (100 milligrams per liter) was clearly the most potent antiethylene treatment. Ag^+ pretreatment inhibited the growth retarding action of 0.2 microliters per liter ethylene by 48% and it also inhibited the incorporation of 0.2 microliters per liter $^{14}C_2H_4$ into pea tips by the same amount. As the ethylene concentration was increased from 0.2 to 30 microliters per liter, the effectiveness of Ag^+ in reducing ethylene action and metabolism declined in a similar fashion. Although Ag^+ significantly inhibited the incorporation of $^{14}C_2H_4$ into tissue metabolites, the oxidation of $^{14}C_2H_4$ to $^{14}CO_2$ was unaffected in the same tissue.

CO_2 (7%) inhibited ethylene-induced growth retardation but its effectiveness diminished at a greater rate than that of Ag^+ with increasing ethylene concentration. High CO_2 had just the opposite effect of Ag^+ since it inhibited $^{14}C_2H_4$ oxidation to $^{14}CO_2$ without affecting tissue incorporation. In contrast to Ag^+, CO_2 did not inhibit ethylene action and metabolism to exactly the same extent, and the inhibition of metabolism did not rapidly decline with increasing $^{14}C_2H_4$ concentration. However, high CO_2 did alter the ratio of $^{14}C_2H_4$ tissue incorporation to $^{14}CO_2$ production in a manner consistent with changes in ethylene effectiveness.

Lowering the O_2 concentration to 5% reduced ethylene-induced growth retardation from 70 to 58% at 0.22 microliters per liter and inhibited $^{14}C_2H_4$ (0.25 microliters per liter) tissue incorporation and oxidation to $^{14}CO_2$ by 26 and 45%, respectively. However, in contrast to Ag^+ and high CO_2 which slightly promoted growth in ethylene-free air, low O_2 reduced pea seedling growth under these conditions thereby severely limiting its usefulness as a specific antiethylene treatment.

Collectively these data suggest that the metabolism of ethylene may be related to its action.

The early work with ^{14}C-labeled ethylene resulted in the general view that ethylene undergoes no permanent chemical change either before, during, or after it accomplishes its biological function (1, 2, 20, 22). More recent work with highly purified $^{14}C_2H_4$ (5) applied to plant tissues under aseptic conditions (3, 4) has made it necessary to change this view since an active ethylene metabolic system has been found in several plant tissues including etiolated pea seedlings (3, 4, 17), carnation (10), and morning glory flowers (12), cotton and bean abscission explants (6), and tomato fruit (unpublished data). This metabolic system exhibits similar characteristics in all tissues so far examined and leads to the incorporation of ethylene into water-soluble tissue metabolites and the oxidation of ethylene to CO_2. The activity of this system and the rate of tissue incorporation relative to oxidation depend on the stage of development (3, 10, 12) and are influenced by such factors as temperature, homogenization, seedling fractionation, O_2, CO_2, COS, and CS_2 (4, 10). Propylene (11) and acetylene (unpublished data) are also metabolized by pea seedlings but at substantially different rates than ethylene. Furthermore, the neutral propylene metabolites formed are chromatographically distinct from those derived from ethylene (11).

Based on this work with purified $^{14}C_2H_4$ it was suggested (4) that ethylene metabolism is an integral part of the ethylene action mechanism. Specifically, the constant metabolic turnover of ethylene in terms of oxidation and/or incorporation at a Cu^+-containing receptor site(s) was proposed as the initial biochemical event in the ethylene action sequence.

Ag^+ (7–9), high CO_2 (2, 14), and low O_2 (2, 14, 15, 19) have all been reported to have antiethylene properties and to reduce ethylene-induced growth retardation in peas. Therefore, these treatments might also be expected to modify ethylene metabolism if as proposed, metabolism is linked to ethylene action. Accordingly, a study was undertaken to compare directly the effect of Ag^+, high CO_2, and low O_2 on ethylene metabolism and action in the etiolated pea seedling.

MATERIALS AND METHODS

Plant Culture. Pea seeds (*Pisum sativum* L. cv. Alaska) stored at 4 C were selected for uniformity in size and color, rinsed in distilled H_2O, and surface-sterilized with constant stirring for 15 min in 1% sodium hypochlorite. After thoroughly rinsing with distilled H_2O the seeds were placed in 4 liters of distilled H_2O for 4 hr at 24 C and the fully imbibed seeds planted in waxed cardboard cups containing Vermiculite (No. 37325, 0.946-liter waxed cups cut in half, Lily-Tulip Cup Corp., New York). Four holes, 5 mm in diameter, were punched in the bottom of each cup for drainage. Seedlings were grown in a 600-liter black growth cabinet of Lucite acrylic resin purged continuously (12 liters min^{-1}) with humidified, ethylene-free air (filtered through Purafil, H. E. Burroughs & Associates, Inc., Chamblee, Ga.). The growth cabinet was located inside a dark room equipped with a green safelight for tissue manipulations. Highly reproducible results were obtained using plant material grown under these carefully controlled conditions.

Ag^+ Experiments. After 4 days, the seedlings in each planting cup were thinned to a uniform stand of 20 seedlings and the length of each epicotyl then measured. Seedlings were sprayed with either 100 mg/l of $AgNO_3$ in distilled H_2O (about 3 ml/cup) or with distilled H_2O only. One planting cup of control seedlings was then placed into each of five 160-mm desiccators sitting in a row

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directly in front of five similar desiccators. Into each of the five dessicators in the second row was placed a cup of $AgNO_3$-treated seedlings. The first pair of desiccators, one containing control seedlings and the other containing $AgNO_3$-treated seedlings, were purged with ethylene-free air while the next four pairs were purged with four different concentrations of ethylene ranging from 0.1 to 30 μl/l in different experiments. Various concentrations of ethylene were obtained by mixing air with ethylene from a gas cylinder containing 6000 μl/l of ethylene. Concentrations of ethylene entering each chamber were determined by gas chromatography. Each feeder line delivering a given ethylene concentration was split just before entering a pair of desiccators to insure that the $AgNO_3$ and control seedlings in each desiccator pair received identical ethylene concentrations. Desiccators were purged at a constant flow rate of 200 cm^3min^{-1}. The gas entering each desiccator was delivered to the bottom of the desiccator which contained approximately 150 ml of water both to humidify the air as it entered the chamber below the surface of the water and to subirrigate the seedlings.

Three separate experiments of this type were conducted. Since each experiment was limited to only four different ethylene concentrations the concentrations were varied from experiment to experiment in order to provide adequate coverage of the wide range in ethylene concentrations used in this study (0.1–30 μl/l). After 2 days of growth in the dark at 24 C the seedlings were removed and the epicotyls remeasured to determine the amount of growth that occurred under the various treatment conditions.

When the seedlings were being sprayed with $AgNO_3$ or distilled H_2O for the growth analysis study additional seedlings from the same planting were also sprayed for subsequent measurement of $^{14}C_2H_4$ metabolism in the pea epicotyl tips. After treatment the intact seedlings were placed in the dark at 24 C for 24 hr. The epicotyl tips were then cut off 10 mm below the top of the hook and 10 tips from control seedlings were placed in each of eight modified Erlenmeyer incubation flasks for $^{14}C_2H_4$ exposure (3, 4). The same number of pea tips from the $AgNO_3$-treated seedlings were placed in eight other flasks. The flasks contained 3 ml of water, a glass stopper, and a side well containing 1 ml of 1.5 N NaOH. Sufficient $^{14}C_2H_4$, purified by preparative gas chromatography (5), was then injected into each flask to yield final $^{14}C_2H_4$ concentrations ranging from 0.2 to 32 μl/l. Eight flasks of control tips were paired with eight flasks of $AgNO_3$-pretreated tips and each pair received a similar amount of $^{14}C_2H_4$ for each of the three experiments. One flask without seedlings was included as a blank for each $^{14}C_2H_4$ concentration as in previous experiments (3, 4). After a 20-hr dark incubation period on a shaker at 24 C the amount of radioactivity trapped in the NaOH or incorporated into the tissue was determined as previously described (3, 4).

CO_2 Experiments. Studies to determine the antiethylene effect of high CO_2 levels on the growth of intact etiolated pea seedlings were conducted in the same gas flow desiccator system used in the Ag^+ experiments. Four-day-old pea seedlings were measured for epicotyl length, placed in the desiccators, and exposed to different concentrations of ethylene in air or elevated CO_2 for 2 days. There was a pair of desiccators for each concentration of ethylene with one desiccator receiving ethylene containing 0.03% CO_2 and the other receiving the same ethylene concentration with 7.0 ± 0.4% CO_2. CO_2 (commercial grade) was metered directly into the inlet line of one of the desiccators of each pair to raise the CO_2 level the desired amount. The seedlings were removed from the desiccators after a 2-day exposure period and then remeasured to determine the antiethylene effect of the added CO_2.

The effect of CO_2 on ethylene metabolism was determined by cutting 5-day-old pea tips as previously described and exposing them to purified $^{14}C_2H_4$ in the presence or absence of CO_2. The flasks without CO_2 contained NaOH at the beginning of the experiment while the flask with CO_2 did not receive NaOH until the end of the experiment. The NaOH was added to the sealed flasks with a hypodermic syringe fitted with a long needle. After NaOH addition the flasks were shaken for 30 min, analyzed for the absence of CO_2, and then all flasks were opened and the NaOH and tissue counted for radioactivity as before (3, 4).

O_2 Experiments. Seedling age and the general experimental design were the same as before except one desiccator in each pair was purged with 5% O_2 while the other received normal levels of O_2. The first two desiccator pairs did not receive ethylene while the next three pairs all received 0.22 μl/l of ethylene. This was accomplished by metering the same amount of ethylene from a 100-μl/l ethylene standard gas cylinder into the 5 and 21% O_2 manifolds supplying the last three desiccator pairs. Final ethylene and O_2 concentrations were determined by gas chromatographic analysis.

The effect of low O_2 on $^{14}C_2H_4$ metabolism was determined by cutting pea tips from 5-day-old seedlings grown for 24 hr in either 5 or 21% O_2 and treating them as before with purified $^{14}C_2H_4$. Immediately upon removing the plants from the air or 5% O_2 pretreatment conditions pea tips were cut and 10 of them were placed into separate flasks as in the Ag^+ experiments. The flasks were then immediately purged with either air or reduced O_2 for 30 min, sealed and injected with purified $^{14}C_2H_4$. Flasks were analyzed for O_2 and ethylene at the beginning and end of each experiment. O_2 levels were adjusted so the final O_2 concentrations never fell below 5%.

RESULTS AND DISCUSSION

Effect of Ag^+. As first observed by Neljubov (21) and subsequently noted by others (2), etiolated pea seedlings are extremely sensitive to ethylene. Generally only about 0.01 μl/l is needed to produce an observable effect on growth, with 0.1 μl/l causing a half-maximal response and no additional inhibition occurring at 10 μl/l and above (1, 2). The inhibition of growth observed in this study for the untreated seedlings was in close agreement with these established dose response relationships (Fig. 1).

As previously reported (9) a single spray application of $AgNO_3$ significantly reduced the responsiveness of the pea seedlings to ethylene. Ag^+-pretreated seedlings exposed to 0.1 μl/l grew nearly twice as tall as the corresponding water controls which were inhibited by 58% (Fig. 1). As the ethylene concentrations was increased the antiethylene effect of Ag^+ diminished until at the highest concentration of 30 μl/l it was hardly detectable. Seedlings pretreated with Ag^+ and placed in ethylene-free air grew only 5% taller than the water controls growing under the same conditions. This indicates that under the normal conditions growth is not severely limited by endogenous ethylene.

The $AgNO_3$ concentration applied in this study was considerably less than that required to inhibit ethylene action maximally

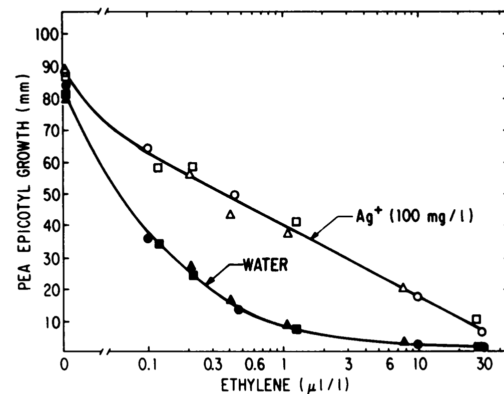


FIG. 1. Effect of Ag^+ in counteracting ethylene-induced growth retardation in etiolated pea seedlings during a 2-day growth period. Data are from three separate experiments.

(9). This lower concentration was used to avoid the slight stimulation of endogenous ethylene production that sometimes occurs at the higher, more effective $AgNO_3$ concentrations of 200 and 300 mg/l (9). Such a stimulation would have reduced the specific activity of the added $^{14}C_2H_4$ in the ethylene metabolism experiments thereby resulting in an apparent reduction in $^{14}C_2H_4$ metabolism. Careful analysis of ethylene production by the treated tissue indicated that this was not a problem at 100 mg/l.

Ag^+ pretreatment had no marked effect on the rate of $^{14}C_2H_4$ oxidation to $^{14}CO_2$ (Fig. 2) although there was a tendency at the lower $^{14}C_2H_4$ concentrations for the Ag^+-pretreated tips to oxidize $^{14}C_2H_4$ at a slightly reduced rate. In contrast to the ineffectiveness of Ag^+ in reducing $^{14}C_2H_4$ oxidation, Ag^+ significantly reduced $^{14}C_2H_4$ tissue incorporation (Fig. 3). This inhibition was the greatest at the lowest concentration of 0.2 μl/l, and it gradually diminished as the $^{14}C_2H_4$ concentration was increased to 32 μl/l. At 0.2 μl/l the rate of incorporation was inhibited by 50% whereas at 2.0 and 20 μl/l this inhibition had declined to 33 and 8%, respectively.

This inhibition was not caused by a toxic heavy metal effect since the conversion of $^{14}C_2H_4$ to $^{14}CO_2$ was essentially unaffected in the same tissue. Also the same concentration of Ag^+ that inhibited $^{14}C_2H_4$ incorporation caused the seedlings to revert to a more normal growth habit in ethylene with no evidence of phytotoxicity (ref. 9 and Fig. 1).

From the data in Figures 1 and 3 the per cent inhibition of ethylene action and tissue incorporation caused by Ag^+ treatment can be calculated (Fig. 4). These profiles of inhibition clearly indicate that a quantitative similarity exists between the inhibitory effect of Ag^+ on ethylene action and tissue incorporation.

Effect of CO_2. Although CO_2 has long been known to antagonize ethylene action in fruit ripening, Burg and Burg (13, 14) were the first to suggest that it was a competitive inhibitor of ethylene action. This proposal was based largely on the results they obtained from double reciprocal plots of the per cent inhibition of pea stem elongation *versus* ethylene concentration at ambient and elevated CO_2 concentrations (14). Since such plots were found to exhibit classical competitive inhibition enzyme kinetics with both curves intersecting at the same point on the ordinate it was proposed that CO_2 competed with ethylene for the same receptor site.

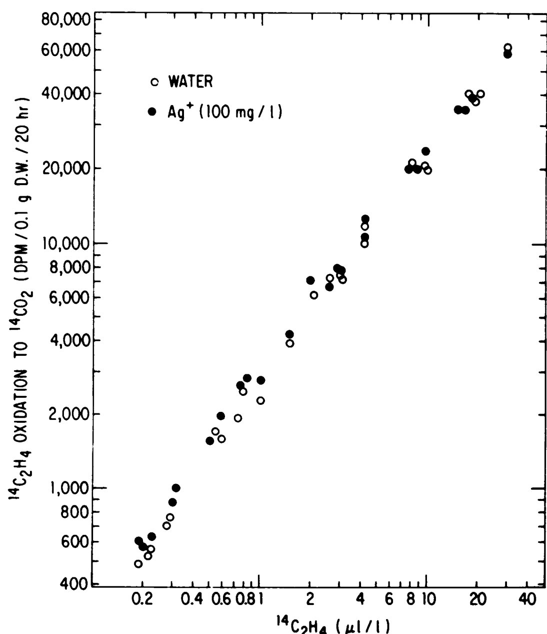


FIG. 2. Effect of Ag^+ on rate of $^{14}C_2H_4$ oxidation to $^{14}CO_2$ in excised pea tips. All data points from three separate experiments have been plotted.

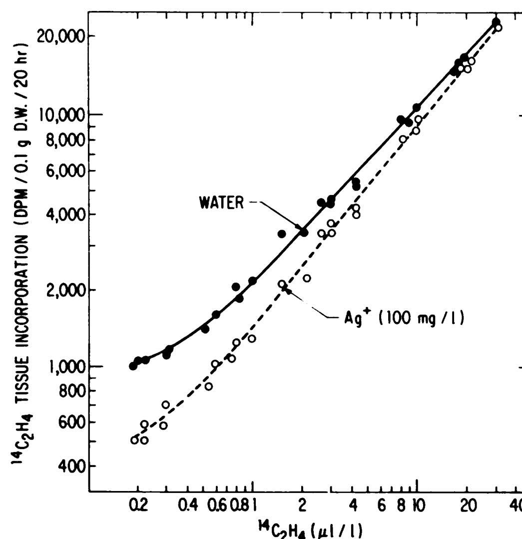


FIG. 3. Effect of Ag^+ on rate of $^{14}C_2H_4$ tissue incorporation in excised pea tips. All data points from three separate experiments have been plotted. Data are from same tissue used in experiments presented in Figure 2.

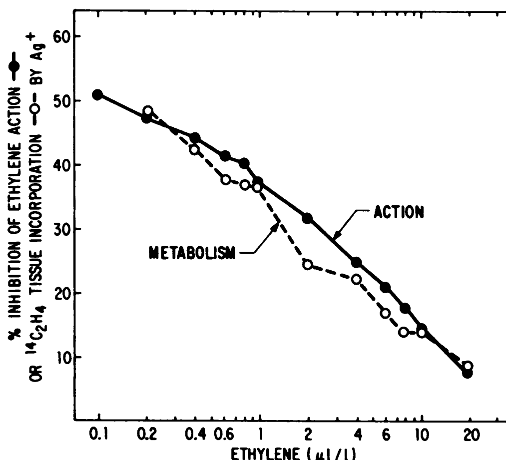


FIG. 4. Per cent inhibition of ethylene action and metabolism by Ag^+. Data derived from Figures 1 and 3.

Similar results were obtained from double reciprocal plots of the data obtained in this study using intact pea seedlings rather than excised subapical sections (data not shown). Only two differences were noted. First, in ethylene-free air 7.0% CO_2 caused a 5 to 10% increase in growth which was not observed by Burg and Burg with excised pea stem sections at 7.1% CO_2 (14). Second, they reported a maximum per cent inhibition of V_m of 50 to 55% whereas in these 2-day experiments with intact seedlings growth was inhibited over 95%. These differences, however, did not alter the competitive inhibition characteristics of the double reciprocal plots.

The most noticeable difference between CO_2 and Ag^+ in the growth analysis experiments was the lack of effectiveness of CO_2 in comparison to Ag^+ at the higher ethylene concentrations. Between 0.1 and 0.4 μl/l the effect of 7.0% CO_2 (data not shown) and 100 mg/l of $AgNO_3$ were very comparable but at concentrations above 0.4 μl/l Ag^+ was much superior. For example, ethylene action was inhibited 30% by Ag^+ at 2 μl/l whereas at the same ethylene concentration the antiethylene effect of CO_2 had disappeared.

CO_2, like Ag^+, inhibited ethylene metabolism but in the opposite manner. With Ag^+, tissue incorporation was inhibited (Fig. 3); oxidation was not inhibited (Fig. 2). In contrast CO_2 uniformly inhibited $^{14}C_2H_4$ oxidation by 65 to 80% at ethylene concentrations ranging from 0.15 to 24 μl/l without having any significant effect on tissue incorporation (Fig. 5). Similar results have been reported for intact pea seedlings (4).

Unlike the results obtained with Ag^+, no clear quantitative relationship was found to exist between the inhibitory effects of CO_2 on ethylene action and metabolism. Another type of relationship was observed, however, that may be significant. This relationship involves the ratio of tissue incorporation to oxidation in the important region below 0.4 μl/l. This region is important because it is where ethylene exerts over 80% of its effect (Fig. 1) and it is the region where the dose response curve for ethylene action is very steep and nearly linear (2). In addition, below 0.4 μl/l $^{14}C_2H_4$: (*a*) the rate of tissue incorporation exceeds that of oxidation (Fig. 5); (*b*) the tissue incorporation curve begins to level off (Figs. 3 and 5); and (*c*) the rate of oxidation rapidly declines relative to tissue incorporation (Figs. 2 and 5).

If in this critical region the rapidly increasing rate of $^{14}C_2H_4$ to $^{14}CO_2$ conversion relative to tissue incorporation were partly responsible for the rapid increase in ethylene effectiveness, then the downward displacement of the entire $^{14}C_2H_4$ oxidation curve by high CO_2 (Fig. 5) would clearly have the effect of reducing ethylene action. Such an effect can be illustrated by comparing the ratio of tissue incorporation to oxidation under conditions with and without added CO_2. At 0.2 μl/l without CO_2 tissue incorporation was 2.4 times faster than oxidation (Fig. 5) and growth was inhibited by 70% (Fig. 1). In contrast, with added CO_2 this same relative ratio of incorporation to oxidation was not established until the ethylene concentration was increased to 0.85 μl/l (Fig. 5) and at this concentration in the presence of 7.0% CO_2 growth was inhibited by nearly the same amount or 66% as determined in the growth analysis experiments (data not shown).

Effect of O_2. O_2 depletion reportedly (15, 19) reduces ethylene sensitivity in fruits, and Burg and Burg (14) observed a similar effect with pea stem sections. With sections, 5% O_2 apparently did not alter O_2 consumption (16), elongation, or CO_2 production (18) but markedly reduced ethylene effectiveness (14). The antiethylene effect of low O_2 was unimpressive (Table I) when compared to CO_2 (14) and Ag^+ (Fig. 1). At 21% O_2 0.22 μl/l of ethylene inhibited growth by 70% as compared to 58% in 5% O_2. This reduction in ethylene effectiveness by 5% O_2 may be somewhat misleading because 5% O_2 also inhibited growth of the intact seedling by 16% in ethylene-free air. This inhibition was clearly different from the results obtained with the more selective inhibitors Ag^+ (Fig. 1) and CO_2 which both slightly increased growth in ethylene-free air.

Low O_2, as opposed to Ag^+ and CO_2, was very nonselective. Whereas both Ag^+ and CO_2 differentially inhibited either $^{14}C_2H_4$ oxidation or incorporation (Figs. 2, 3, and 5), low O_2 inhibited both (Table II). The degree of inhibition was greater for oxidation (45%) than for tissue incorporation (26%). Since 5% O_2 inhibited growth in ethylene-free air, part of this inhibition was probably due to a general adverse effect on cellular metabolism.

CONCLUSIONS

If ethylene action and metabolism are related, a change in ethylene responsiveness should be accompanied by a corresponding change in ethylene metabolism. In general this was found to be the case since Ag^+, high CO_2 and low O_2 all inhibited ethylene-induced growth retardation and ethylene metabolism in the etiolated pea. The remarkable quantitative relationship found between the effect of Ag^+ on ethylene action and metabolism provides indirect evidence in support of the ethylene metabolism-action hypothesis (4). However the results with high CO_2 and low O_2 were less clear-cut. Although both inhibited ethylene action and metabolism, no simple quantitative relationship was found to exist between their effects on metabolism and action. Although circumstantial evidence obtained in this and other studies (3, 4, 10, 12) suggests that ethylene action and metabolism may be related, additional evidence is clearly needed to reinforce this point.

Regardless of the functional connection that may exist between ethylene action and metabolism, it is apparent from this study that the ethylene metabolic system is relatively complex, consisting of not a single pathway but one involved in the incorporation of ethylene and another responsible for the oxidation of ethylene to CO_2. This must be true since Ag^+ and high CO_2 were capable of selectively inhibiting one pathway without affecting the other. A simplified scheme for ethylene metabolism is shown in Figure 6. Oxidation and incorporation are depicted as two separate, but possible interrelated processes. The ratio of one to the other is not constant but changes markedly depending on the type of tissue,

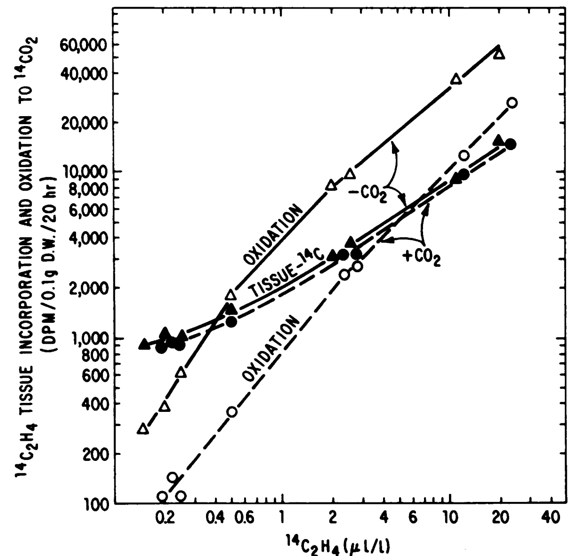


FIG. 5. Effect of 7% CO_2 on $^{14}C_2H_4$ metabolism in excised pea tips. Data are from one experiment. Similar results were obtained in two other experiments.

TABLE I. Effect of Ethylene (0.22 μl/l) on Growth of Intact Peas in Air and 5% O_2.

	Epicotyl Length (mm)					
	21% O_2			5% O_2		
	$-C_2H_4$	$+C_2H_4$	% Red	$-C_2H_4$	$+C_2H_4$	% Red
Exp. I	82	25		68	27	
Exp. II	78	22		65	28	
Ave.	80	24	70	67	28	58

TABLE II. Effect of 5% O_2 on $^{14}C_2H_4$ Metabolism at an Applied Concentration of 0.25 μl/l (DPM/0.1 gm D.W./20 hr).

	Tissue Incorporation			Oxidation		
	Air	5% O_2	% Red	Air	5% O_2	% Red
Exp. I	1150	850		550	300	
Exp. II	1200	880		590	330	
Ave.	1175	865	26	570	315	45

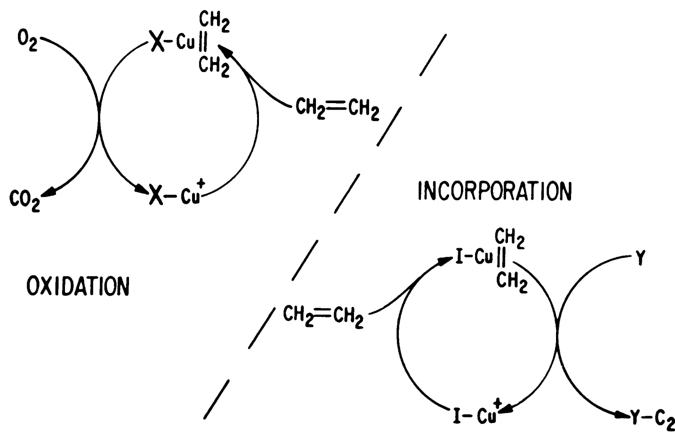
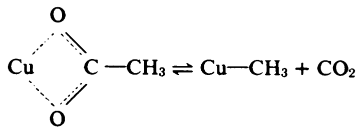


FIG. 6. Scheme for ethylene metabolism.

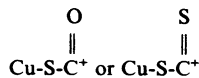
the stage of development, and the ethylene concentration (3, 10, 12).

As previously reported (4) the receptor site is believed to contain Cu^+. Initially Ag^+ was thought to alter ethylene action by substituting for Cu^+ at the receptor site. This seemed reasonable since Ag^+ and Cu^+ have the same valence, are of similar size, and are known to form complexes with ethylene. Because of differences in their binding constants with ethylene the receptor site reaction might be reduced under conditions where Ag^+ would substitute for Cu^+. Inasmuch as Ag^+ was found to inhibit only ethylene incorporation and not oxidation in this study this hypothetical substitution of Ag^+ for Cu^+ now seems unlikely unless Ag^+ were to interfere selectively with only the incorporation site. Perhaps this would be possible if the oxidation site contained tightly bound Cu^+ while the incorporation site did not. Alternatively, tissue incorporation may involve Cu^+ whereas the oxidation pathway may not.

CO_2 is a product of the oxidation reaction. The ability of high CO_2 levels to inhibit this process selectively could possibly involve some type of feedback inhibition or mass action effect, *e.g.*



COS and CS_2, analogs of CO_2 which inhibit both ethylene oxidation and tissue incorporation (10), are thought to act by reacting with Cu^+ to form



The model presented for ethylene metabolism has several features in common with the scheme proposed earlier by Burg and Burg (13) for ethylene action. They first proposed that ethylene binds to a metallic-containing receptor site (metalloenzyme) and that O_2 and ethylene interact at this site in some way to activate it. In this regard the oxidation pathway of the ethylene metabolism model is quite similar. From this point on, however, the two schemes are conceptually very different since the Burgs (13) visualized ethylene as acting strictly as an activator molecule and undergoing no chemical change whereas in the present scheme ethylene metabolism is considered an integral part of the ethylene action sequence. As with the Burgs' earlier scheme, the key changes brought about by these initial events are still entirely unknown.

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LITERATURE CITED

1. ABELES FB 1972 Biosynthesis and mechanism of action of ethylene. Annu Rev Plant Physiol 23: 259-292
2. ABELES FB 1973 Ethylene in Plant Biology. Academic Press, New York
3. BEYER EM JR 1975 ^{14}C-ethylene incorporation and metabolism in pea seedlings. Nature 255: 144-147
4. BEYER EM, JR 1975 $^{14}C_2H_4$: its incorporation and metabolism by pea seedlings under aseptic conditions. Plant Physiol 56: 273-278
5. BEYER EM JR 1975 $^{14}C_2H_4$: its purification for biological studies. Plant Physiol 55: 845-848
6. BEYER EM JR 1975 Ethylene-^{14}C metabolism during abscission. Proc. 29th Beltwide Cotton Production Research Conference. New Orleans, La. pp 51-52
7. BEYER EM JR 1976 Ethylene antidote. HortScience 11: 174
8. BEYER EM JR 1976 Silver ion: a potent antiethylene agent in cucumber and tomato. HortScience 11: 195-196
9. BEYER EM JR 1976 A potent inhibitor of ethylene action in plants. Plant Physiol 58: 268-271
10. BEYER EM JR 1977 $^{14}C_2H_4$: its incorporation and oxidation to $^{14}CO_2$ by cut carnations. Plant Physiol 60: 203-206
11. BEYER EM JR 1978 Rapid metabolism of propylene by pea seedlings. Plant Physiol 61: 893-895
12. BEYER EM JR, O SUNDIN 1978 $^{14}C_2H_4$ metabolism in morning glory flowers. Plant Physiol 61: 896-899
13. BURG SP, EA BURG 1965 Ethylene action and the ripening of fruits. Science 148: 1190-1196
14. BURG SP, EA BURG 1967 Molecular requirements for the biological activity of ethylene. Plant Physiol 42: 144-152
15. DENNY FE 1924 Hastening the coloration of lemons. J Agric Res 27: 757-769
16. EICHENBERG E, KV THIMANN 1957 Terminal oxidases and growth in plant tissues. Arch Biochem Biophys 67: 466-769
17. GIAQUINTA R, EM BEYER JR 1977 $^{14}C_2H_4$: distribution of ^{14}C-labeled tissue metabolites in pea seedlings. Plant Cell Physiol 18: 141-148
18. HACKETT DP, HA SCHNEIDERMAN 1953 Terminal oxidases and growth in plant tissues. Arch Biochem Biophys 47: 190-204
19. KIDD F, C WEST 1945 Respiratory activity and duration of life of apples gathered at different stages of development and subsequently maintained at a constant temperature. Plant Physiol 20: 467-504
20. MCGLASSON WB 1970 Biochemistry of fruits and their products. Food Sci Technol Monogr Series. Academic Press, New York
21. NELJUBOV DN 1901 Ueber die horizontal Nutation der Stengel von *Pisum sativum* und einiger anderen Pflanzen. Beih Bot Zentralbl 10: 128-139
22. VARNER JE, DT HO 1976 Plant Biochemistry, Ed 3. Academic Press, New York