Metabolism of Cyclopropanecarboxylic Acid

A NEW ROLE FOR CARNITINE*

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SUMMARY

The fungus Fusarium oxysporum converts cyclopropanecarboxylic acid to \( \gamma \)-hydroxybutyric acid through the intermediate cyclopropanecarboxylate-X, a derivative of cyclopropanecarboxylic acid (Schiller, J. G., and Chung, A. E. (1970) J. Biol. Chem. 245, 5857).

Inclusion of DL-carnitine in the incubation mixture of whole cells of the fungus with [\( \text{L-}^{14}\text{C}\)]cyclopropanecarboxylic acid resulted in an increase in the amount of [\( \text{L-}^{14}\text{C}\)]cyclopropanecarboxylate-X synthesized. Authentic [\( \text{L-}^{14}\text{C}\)]cyclopropanecarboxylate-X was identified in the fungus Cyclopropanecarboxylate DL-carnitine is converted by cell-free extracts of the fungus to \( \gamma \)-hydroxybutyric acid as is cyclopropanecarboxylate-X. These results indicate that the intermediate cyclopropanecarboxylate-X is cyclopropanecarboxylate carnitine.

Cells of the fungus Fusarium oxysporum Schlechtendahl grown on cyclopropanecarboxylic acid as sole carbon source convert cyclopropanecarboxylic acid to \( \gamma \)-hydroxybutyric acid through the intermediate cyclopropanecarboxylate-X (1). This derivative can be converted to \( \gamma \)-hydroxybutyric acid by cell-free extracts of the fungus. Preliminary investigation of the chemical properties of cyclopropanecarboxylate-X revealed that mild acidic or basic hydrolysis resulted in release of the intact cyclopropylcarbonyl moiety. Ion exchange chromatography indicated that the derivative contained a positive charge. In this study the partial purification of cyclopropanecarboxylate-X will be described and evidence will be presented that indicates that this derivative is cyclopropanecarboxylate carnitine.

MATERIALS AND METHODS

Sephadex LH-20 was obtained from Pharmacia. DL-Carnitine hydrochloride, acetylcoenzyme A, and phenylmethylsulfonyl fluoride were obtained from Sigma. Jenden’s reagent, a mixture of sodium benzene thiolate and benzene thiol in anhydrous butanone, was obtained from Applied Science. Carnitine estertransferase was obtained from Boehringer Mannheim. All other materials were obtained as previously described (1).

Growth of F. oxysporum Schlechtendahl—The microorganism was grown on cyclopropanecarboxylic acid in a basic salts medium as previously described (1). In some experiments, cyclopropanecarboxylic acid was replaced by \( \gamma \)-hydroxybutyrate as the sole carbon source. The concentration of this compound was 0.2 g/100 ml of basic salts medium.

Incubation of F. oxysporum Cells with [\( \text{L-}^{14}\text{C}\)]Cyclopropanecarboxylic Acid—Cells grown on \( \gamma \)-hydroxybutyrate were harvested and processed by a modification of the method of Schiller and Chung (1). The harvested cells were incubated for predetermined times with [\( \text{L-}^{14}\text{C}\)]cyclopropanecarboxylic acid in carbon-free growth medium, collected, and washed rapidly with cold water on a Buchner funnel. The cellular mat was processed through the acetone extraction and centrifugation step previously described (1).

The 105,000 × g supernatant solutions obtained from the acetone powder extract and acetone extract were pooled and concentrated under reduced pressure at 44° to 50 ml. An equal volume of methanol was added and the suspension was stored at 4° overnight. The suspension was concentrated under reduced pressure at 44° to remove the methanol. The supernatant, obtained by centrifugation at 35,000 × g for 15 min was concentrated to 2 ml as previously described in preparation for Sephadex G-10 chromatography.

Incubation of F. oxysporum Cells with [\( \text{L-}^{14}\text{C}\)]Cyclopropanecarboxylic Acid and DL-Carnitine—The incubation procedures used were similar to those described above except that an incubation time of 30 s was used and varying amounts of DL-carnitine were included in the incubation medium.

Preparation of Cell Extracts of F. oxysporum—The general method of Schiller and Chung (1) was used with the following modifications. Forty milliliters of 0.1 M potassium phosphate buffer, pH 6.5, at 0° were added to the beaker containing rapidly frozen cells, wet weight 20 g. A sample, 0.6 ml of 1.6% phenylmethylsulfonylfluoride in isopropyl alcohol was added to inhibit proteolytic enzymes. The cell suspension was subjected to sonic oscillation in eight 20-s pulses with a Heat Systems sonifier at a setting of 70% of maximal power. The temperature of the suspension did not increase above 10° during this treatment. The mixture was centrifuged for 15 min at 35,000 × g and the super-

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Purification of Cyclopropanecarboxylate-X—The concentrated sample obtained from incubation of *F. oxysporum* cells with [1-14C]cyclopropanecarboxylic acid was applied to a column, 1.6 x 90 cm, of Sephadex G-10. The column was maintained at 4°C and pre-equilibrated with 0.05 M potassium phosphate buffer, pH 7.0. The column was developed with the equilibrating buffer by a flow rate of 20 ml per hour. Fractions were collected at 6-min intervals and 0.1-ml samples assayed for radioactivity as previously described (1). The fractions containing cyclopropanecarboxylate-X, as determined by the elution volume, were pooled and concentrated under reduced pressure to a final volume of 2 ml.

The concentrated sample was placed in a centrifuge tube and 2 volumes of methanol were added, followed by 10 volumes of acetone. This mixture was centrifuged at 35,000 x g for 15 min in a Sorvall RC2-B refrigerated centrifuge equipped with an SS-1 rotor. The supernatant solution from this precipitation step was evaporated to dryness and the residue was taken up in 2 ml of isopropyl alcohol-pyridine-water (2:1:1) in preparation for Sephadex LH-20 chromatography.

A column, 1.4 x 62 cm, of Sephadex LH-20, equilibrated with isopropyl alcohol-pyridine-water (2:1:1) was packed at room temperature. The sample from the precipitation step was applied to the column and the column was eluted with the equilibrating solvent. The flow rate was maintained at 10 ml per hour. Fractions were collected at 10-min intervals. The column effluent was monitored for radioactivity by assaying 0.02-ml samples of each fraction. The fractions containing cyclopropanecarboxylate-X from this column were evaporated to near-dryness under reduced pressure and the residue was taken up in 2 ml of water in preparation for Sephadex G-10 chromatography.

The sample from the Sephadex LH-20 step was chromatographed at 4°C on a Sephadex G-10 column, 1.6 x 90 cm, equilibrated, and developed with glass-distilled water. The flow rate was 20 ml per hour and fractions were collected at 6-min intervals. The fractions were monitored for radioactivity and 260-nm absorbance. The radioactive fractions were pooled, centrifuged, and rechromatographed on Sephadex G-10 until the radioactive and ultraviolet-absorbing peaks were resolved. The purification procedure is summarized in Table I. The final samples of cyclopropanecarboxylate-X were used for mass spectral analysis.

**Synthesis of [1-14C]Cyclopropanecarboxylate dl-Carnitine—** Labeled cyclopropanecarboxylate dl-carnitine was synthesized according to the method of Duncombe and Rising (2). Cyclopropanecarboxylic acid (0.215 g, 2.53 mmoles; specific activity 23.6 μCi per mmole) was heated under reflux, protected from atmospheric moisture, at 80°C in a water bath with triethanol chloride (0.297 g, 2.53 mmoles). dl-Carnitine hydrochloride (0.166 g, 0.84 mmole) dissolved in 0.75 ml of trifluoroacetic acid was added to the acid chloride solution. The reaction mixture, protected from atmospheric moisture, was heated at 50-55°C in a water bath with occasional shaking for 2 hours. The solution was cooled to room temperature and 0.5 ml of methanol was added to decompose any excess acid chloride. Acetone, 5 volumes, was added to precipitate unreacted carnitine. The suspension was filtered after standing overnight at room temperature. Ethyl ether was added to the suspension to 4°C overnight. The suspension was filtered and the precipitate was dissolved in 2 ml of distilled water.

The aqueous solution was further purified by chromatography on a Sephadex G-10 column, equilibrated with water, as described under "Purification of Cyclopropanecarboxylate-X." Fractions were assayed for radioactivity as described above. Those fractions containing labeled cyclopropanecarboxylate dl-carnitine were pooled and concentrated. The retention volume of cyclopropanecarboxylate dl-carnitine was 87 ml. Overall recovery was 15 to 105 cpm or 0.3 mmole based on the specific activity of 23.6 μCi per mmole. The yield was 30% based on the amount of dl-carnitine initially added. This aqueous concentrate of cyclopropanecarboxylate dl-carnitine was utilized in the metabolic and chemical studies.

**RESULTS**

Factors Affecting Formation of Cyclopropanecarboxylate-X—The cyclopropanecarboxylate X formed after incubation of *Fusarium* cells with [1-14C]cyclopropanecarboxylic acid was monitored by its characteristic elution volume and radioactivity when the reaction products were chromatographed on Sephadex G-10 as described previously (1). Cells grown on cyclopropanecarboxylic acid and incubated with [1-14C]cyclopropanecarboxylic acid yielded a complex pattern of radioactive compounds. If the incubation time was increased beyond 10 s, the cyclopropanecarboxylate-X peak became obscured by terminal degradation products formed after incubation of the cells with substrate for up to 2 min. As shown in Table II the uptake of radioactivity into this product increased with time of incubation. Furthermore, as the time of incubation was increased from 10 s to 1 min, the total amount of label incorporated into the cells increased from 0.6 and 0.8% to 1.3% of the radioactivity initially added. Since the total amount of label taken up by the cyclo-

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**Table I**

| Method | Total recovered radioactivity | Yield of recovered radioactivity |
|--------|------------------------------|---------------------------------|
|        | Exp. 1 | Exp. 2 | Exp. 1 | Exp. 2 |
| 1. Sephadex G-10; 0.05 M PO4 buffer, pH 7.0 | 1,324,000 | 470,000 | 100 | 100 |
| 2. Methanol-acetone precipitation | 711,000 | | |
| 3. Sephadex LH-20; isopropyl alcohol-pyridine-water (2:1:1) | 783,000 | 385,000 | 50 | 82 |
| 4. Sephadex G-10; water | 415,000 | | |
| 5. Sephadex G-10; water | 395,000 | | |
| 6. Sephadex G-10; water | 344,000 | | |
The increased formation of cyclopropanecarboxylate-X by cells grown on cyclopropanecarboxylic acid was monitored for radioactivity as described under "Materials and Methods." The wet weight of cells utilized was 22.5 g. The column effluent was monitored for radioactivity as described under "Materials and Methods." The presence of m-carnitine, however, did not significantly affect the relative proportions of cyclopropanecarboxylate-X and cyclopropanecarboxylic acid present in the cellular extract, since the cyclopropanecarboxylate-X fractions contain approximately three-fourths of the label taken up by the whole cells in all three of the above cases. Further increases in the m-carnitine concentration above 5 mM resulted in a decrease in the amount of cyclopropanecarboxylate-X synthesized, but the amount of label taken up remained relatively constant. Presumably the L isomer of carnitine is the biologically active one in this system. At higher concentrations of carnitine the unnatural D isomer may be inhibiting the formation of cyclopropanecarboxylate-X.

Comparison of Chemical and Biological Properties of Cyclopropane-carboxylate-X and Cyclopropane-carboxylate m-Carnitine—The observation that the presence of m-carnitine stimulated the synthesis of cyclopropane-carboxylate-X indicated that X might be carnitine. The [1-14C]cyclopropanecarboxylic acid ester of m-carnitine was tested by incubation of this compound with cell-free extracts from cyclopropanecarboxylic acid-grown cells. The observation that the presence of m-carnitine strongly stimulated the synthesis of cyclopropane-carboxylate-X with a proportionate increase in the amount of label taken up by the cells. Increasing the amount of m-carnitine to 5 mM again increased the amount of cyclopropane-carboxylate-X synthesized and also increased the uptake of label. The procedure was as described under "Materials and Methods." The procedure was as described under "Materials and Methods."

### TABLE II

**Synthesis of cyclopropanecarboxylic acid-X from [1-14C]cyclopropanecarboxylic acid as function of incubation time of y-hydroxybutyric acid-grown Fusarium oxysporum cells**

The procedure was as described under "Materials and Methods."

| Time of incubation | Radioactivity incorporated per 15 g cells | Radioactivity in CPCA-X fraction per 15 g cells |
|--------------------|------------------------------------------|-----------------------------------------------|
| 10 s               | 0.85 %                                   | 360,000                                       |
| 15 s               | 0.54 %                                   | 480,000                                       |
| 30 s               | 0.75 %                                   | 605,000                                       |
| 1 min              | 1.35 %                                   | 1,320,000                                     |
| 2 min              | 1.30 %                                   | 1,080,000                                     |

* CPCA-X, cyclopropanecarboxylic acid-X.
* Average of three runs with a range of 0.60 to 0.89% per 15 g cells.
* Average of three runs with a range of 468,000 to 785,000 cpm per 15 g cells.

### TABLE III

**Effect of added m-Carnitine hydrochloride on synthesis of cyclopropanecarboxylic acid-X from [1-14C]cyclopropanecarboxylic acid on incubation for 30 s with Fusarium oxysporum cells**

The procedure was as described under "Materials and Methods." The presence of 2.5 mM m-Carnitine strongly stimulated the synthesis of cyclopropanecarboxylate-X with a proportionate increase in the amount of label taken up by the cells. Increasing the amount of m-Carnitine to 5 mM again increased the amount of cyclopropane-carboxylate-X synthesized and also increased the uptake of label. The procedure was as described under "Materials and Methods." The procedure was as described under "Materials and Methods."

| m-Carnitine hydrochloride | Radioactivity in CPCA-X fraction per 15 g cells | Radioactivity incorporated per 15 g cells |
|---------------------------|-------------------------------------------------|-----------------------------------------|
| 0                         | 603,000*                                        | 0 %*                                    |
| 2.5                       | 1,836,000                                       | 2.0 %                                   |
| 5.0                       | 3,325,000                                       | 5.1 %                                   |
| 10.0                      | 1,085,000                                       | 3.6 %                                   |
| 35.0                      | 1,158,000                                       | 6.4 %                                   |

* CPCA-X, cyclopropanecarboxylic acid-X.
* Average of three runs.

with labeled cyclopropanecarboxylic acid in the presence of varying amounts of m-Carnitine was explored and the results of these experiments are summarized in Table III. The presence of 2.5 mM m-Carnitine strongly stimulated the synthesis of cyclopropanecarboxylate-X with a proportionate increase in the amount of label taken up by the cells. Increasing the amount of m-Carnitine to 5 mM again increased the amount of cyclopropane-carboxylate-X synthesized and also increased the uptake of label. The procedure was as described under "Materials and Methods." The procedure was as described under "Materials and Methods."

### TABLE IV

**Comparison of Chemical and Biological Properties of Cyclopropane-carboxylate-X and Cyclopropane-carboxylate m-Carnitine**

The observation that the presence of m-Carnitine stimulated the synthesis of cyclopropane-carboxylate-X indicated that X might be carnitine. The [1-14C]cyclopropanecarboxylic acid ester of m-Carnitine was tested by incubation of this compound with cell-free extracts from cyclopropane-carboxylic acid-grown cells. The observation that the presence of m-Carnitine strongly stimulated the synthesis of cyclopropane-carboxylate-X with a proportionate increase in the amount of label taken up by the cells. Increasing the amount of m-Carnitine to 5 mM again increased the amount of cyclopropane-carboxylate-X synthesized and also increased the uptake of label. The procedure was as described under "Materials and Methods." The procedure was as described under "Materials and Methods." The procedure was as described under "Materials and Methods." The procedure was as described under "Materials and Methods."

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| 10.0                      | 1,085,000                                       | 3.6 %                                   |
| 35.0                      | 1,158,000                                       | 6.4 %                                   |

* CPCA-X, cyclopropanecarboxylic acid-X.
* Average of three runs.

The retention volumes on Sephadex G-10 and LH-20
The organism *F. oxysporum* can degrade the cyclopropane ring of cyclopropanecarboxylic acid in order to fulfill its metabolic requirements. The sequence of reactions involved in the degradation of cyclopropanecarboxylic acid involve an "activation" of cyclopropanecarboxylic acid to cyclopropanecarboxylate-X.

Increased amounts of cyclopropanecarboxylate-X were obtained by utilizing γ-hydroxybutyrate instead of cyclopropanecarboxylic acid as sole carbon source for growth of *F. oxysporum*. Cyclopropanecarboxylate-X was obtained in radiopure form, but was not chemically pure as determined by mass spectral analysis. Enzymatic assay of a hydrolyzed sample of the compound indicated the presence of L-carnitine in the products of hydrolysis, but the molar ratio of L-carnitine to cyclopropanecarboxylate was less than unity. Investigation of the chemical properties of radiopure cyclopropanecarboxylic acid-X further indicated X could be due to the fact that the assay was being run at its lower level of sensitivity and furthermore the method will detect only the L isomer of carnitine.

**Discussion**

A sample of cyclopropanecarboxylate-X was subjected to basic hydrolysis and the products analyzed for the presence of L-carnitine by the spectrophotometric method of Fritz and Schultz (6). The assay indicated the presence of approximately 3 nmoles of L-carnitine in a sample which contained approximately 12 nmoles of cyclopropanecarboxylate-X based upon its radioactivity. The L-carnitine was formed only after hydrolysis since the unhydrolyzed sample contained no L-carnitine. The somewhat low yield could be due to the fact that the assay was a little low yield could be due to the fact that the assay was a little low yield could be due to the fact that the assay was a little low yield could be due to the fact that the assay was

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**Table IV**

| Chromatographic system | Compound          | Retention volume | Relative migration |
|------------------------|-------------------|------------------|-------------------|
| 1. Sephadex G-10<sup>a</sup> | CPCA-X            | 86               |                   |
| 2. Sephadex LH 20<sup>a</sup> | CPCA-carnitine    | 86               |                   |
| 3. Sephadex LH 20<sup>a</sup> | CPCA-X            | 70               |                   |
| 4. Sephadex LH 20<sup>a</sup> | CPCA-carnitine    | 70               |                   |
| 5. Sephadex LH 20<sup>a</sup> | CPCA-X            | 68               | 0.41              |
| 6. Sephadex LH 20<sup>a</sup> | CPCA-carnitine    | 68               | 0.44              |
| 7. Sephadex LH 20<sup>a</sup> | CPCA-X            | 68               | 0.46              |
| 8. Sephadex LH 20<sup>a</sup> | CPCA-carnitine    | 68               | 0.46              |

<sup>a</sup> Procedure was as described under "Materials and Methods."  
<sup>b</sup> CPCA, cyclopropanecarboxylic acid.  
<sup>c</sup> Solvent system used was EtOH-H<sub>2</sub>O-concentrated NH<sub>4</sub>OH (90:5:5).  
<sup>d</sup> Solvent system used was EtOH-H<sub>2</sub>O-concentrated NH<sub>4</sub>OH (95:5:4).  
<sup>e</sup> Solvent system used was CHCl<sub>3</sub>-MeOH-H<sub>2</sub>O-concentrated NH<sub>4</sub>OH-HCOOH (85:5:10:7.5:2.5).  
<sup>f</sup> Solvent system used was EtOH-H<sub>2</sub>O-concentrated NH<sub>4</sub>OH (96:25:4).

![Fig. 2. Metabolism of cyclopropanecarboxylate DL-carnitine and cyclopropanecarboxylic acid-X by cell-free extracts of *Fusarium oxysporum*. (a) The cell-free sonicate was obtained as described under "Materials and Methods." and contained 6.85 mg of protein per ml. Ten milliliters of cell extract were added to 1.12 

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**DISCUSSION**

The organism *F. oxysporum* can degrade the cyclopropane ring of cyclopropanecarboxylic acid in order to fulfill its metabolic requirements. The sequence of reactions involved in the degradation of cyclopropanecarboxylic acid involve an "activation" of cyclopropanecarboxylic acid to cyclopropanecarboxylate-X.

Increased amounts of cyclopropanecarboxylate-X were obtained by utilizing γ-hydroxybutyrate instead of cyclopropanecarboxylic acid as sole carbon source for growth of *F. oxysporum*. Cyclopropanecarboxylate-X was obtained in radiopure form, but was not chemically pure as determined by mass spectral analysis. Enzymatic assay of a hydrolyzed sample of the compound indicated the presence of L-carnitine in the products of hydrolysis, but the molar ratio of L-carnitine to cyclopropanecarboxylate was less than unity. Investigation of the chemical properties of radiopure cyclopropanecarboxylic acid-X further indicated X could be due to the fact that the assay was being run at its lower level of sensitivity and furthermore the method will detect only the L isomer of carnitine.

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| 3. Sephadex LH 20<sup>a</sup> | CPCA-X            | 70               |                   |
| 4. Sephadex LH 20<sup>a</sup> | CPCA-carnitine    | 70               |                   |
| 5. Sephadex LH 20<sup>a</sup> | CPCA-X            | 68               | 0.41              |
| 6. Sephadex LH 20<sup>a</sup> | CPCA-carnitine    | 68               | 0.44              |
| 7. Sephadex LH 20<sup>a</sup> | CPCA-X            | 68               | 0.46              |
| 8. Sephadex LH 20<sup>a</sup> | CPCA-carnitine    | 68               | 0.46              |

<sup>a</sup> Procedure was as described under "Materials and Methods."  
<sup>b</sup> CPCA, cyclopropanecarboxylic acid.  
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<sup>f</sup> Solvent system used was EtOH-H<sub>2</sub>O-concentrated NH<sub>4</sub>OH (96:25:4).
chondrial incubation medium, a 4-fold increase in this metabolite was noted.

Attempts to volatilize cyclopropanecarboxylate-X and cyclopropanecarboxylate DL-carnitine for gas chromatographic-mass spectral analysis were made utilizing Jenden's reagent (7), but, under conditions of the reaction, hydrolysis of the cyclopropanecarboxylate esters occurred. Both molecules are adsorbed on Dowex 50 cation exchange resin; however, neither was eluted with 3 N hydrochloric acid.

Cell-free extracts of cyclopropanecarboxylate-grown F. oxysporum cells convert both cyclopropanecarboxylate-X and cyclopropanecarboxylate DL-carnitine to γ-hydroxybutyrate and cyclopropanecarboxylic acid. Cyclopropanecarboxylate-X is completely metabolized by the cell-free extract, while cyclopropanecarboxylate DL-carnitine is not. Presumably the unnatural D isomer would not be metabolized by the enzyme system. The amount of cyclopropanecarboxylate DL-carnitine remaining is close to the theoretical 50% expected (see Fig. 2). Also, the specific activity of cyclopropanecarboxylate DL-carnitine was lower than that for cyclopropanecarboxylate-X and a greater concentration of cyclopropanecarboxylate DL-carnitine was used than was used for cyclopropanecarboxylate-X (see legend to Fig. 2). However a 10 to 100-fold excess in concentration of cyclopropanecarboxylate DL-carnitine over that of cyclopropanecarboxylate-X gave essentially the same proportion of cyclopropanecarboxylate DL-carnitine remaining, indicating the enzyme system was not saturated with cyclopropanecarboxylate DL-carnitine. Extracts of cells stored frozen for prolonged periods were able to hydrolyze only a small amount of either substrate to cyclopropanecarboxylic acid. Cell-free extracts that do not metabolize cyclopropanecarboxylate-X to γ-hydroxybutyrate did not metabolize cyclopropanecarboxylate DL-carnitine, and extracts that do metabolize cyclopropanecarboxylate-X to γ-hydroxybutyrate also metabolize cyclopropanecarboxylate DL-carnitine to γ-hydroxybutyrate.

The above observations are consistent with the postulate that cyclopropanecarboxylate-X is cyclopropanecarboxylate DL-carnitine and that "activation" of cyclopropanecarboxylic acid to cyclopropanecarboxylate DL-carnitine occurs in whole cells.

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