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Response of *Zea mays* and *Lycopersicon esculentum* to the ethylene precursors, L-methionine and L-ethionine applied to soil

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Abstract

Glasshouse experiments were conducted to evaluate the influence of L-methionine (L-MET) and L-ethionine (L-ETH) added to soil on the growth of corn (*Zea mays* L.) and tomato (*Lycopersicon esculentum*), respectively. The application of L-MET and L-ETH stimulated C_2H_4 production in soil by 299- and 313-fold, respectively, over an unamended control. An L-MET treatment of 1.85 mg kg^{-1} soil was the most effective in increasing shoot height, shoot fresh weight, internodal distance, and stem diameter in two corn cultivars, Kandy Korn and Miracle, while shoot and root dry weights, leaf width, uppermost leaf collar base distance and resistance to stem breaking were increased in the case of Kandy Korn only. A significant epinastic response was observed in the second and third leaves of tomato plants when soil was treated with L-ETH. An L-ETH treatment of 0.2 mg kg^{-1} soil resulted in the maximum fresh fruit yield, while 0.02 and 2.0 mg kg^{-1} gave the most fruit and greater average weight of fresh fruit, respectively. Concentrations ranging from 0.002 to 2.0 mg L-ETH kg^{-1} soil initiated early fruit formation. Early fruit ripening was observed with an application rate of 20 mg L-ETH kg^{-1} soil. The mechanism of action of these chemicals could either be attributed to i) substrate-dependent C_2H_4 production in soil by the indigenous microflora, ii) uptake directly by plant roots followed by metabolism within the tissues, and/or iii) a change in the balance of rhizosphere microflora affecting plant growth.

Introduction

Ethylene (C_2H_4) is a potent endogenous plant hormone which exerts a major influence on many aspects of plant growth and development. It has been identified as a common constituent of the soil atmosphere as a result of microbial activity (Smith and Cook, 1974; Smith and Restall, 1971). According to Primrose (1979), microbial production of C_2H_4 could have an impact on crop production under certain management conditions since C_2H_4 concentrations as low as 10 $\mu g\ L^{-1}$ can evoke plant responses and a concentration of 25 $\mu g\ L^{-1}$ affects fruit and flower development. Similarly, direct application of C_2H_4 gas to roots has been shown to have a direct influence on rice, barley, rye, cotton, sorghum, tomato, pea, white clover, and white mustard, depending on the concentration applied (Crossett and Campbell, 1975; Fretag *et al.*, 1972; Goodlass and Smith, 1979; Ishizawa and Esashi, 1984; Imaseki and Pjon, 1970; Jackson and Campbell 1975; Konings and Jackson, 1979; Ku *et al.*, 1970; Smith and Robertson, 1971). Soil drenched or foliarly-applied ethephon affects the growth of tomato, wheat, barley and maize (Dahnous *et al.*, 1982; Kuo and Chen, 1980; Langan and Oplinger, 1987). A recent review on the microbial production of C_2H_4 in soil and its impact on plant growth indicates the agronomic importance of this plant hormone (Arshad and Frankenberger, 1990a;b). Ethylene biosynthesis and its regulation in higher plants has been reviewed by Yang and Hoffman (1984).

Soil contains an appreciable number of fungi

(Ilag and Curtis, 1968; Lynch and Harper, 1974) and bacteria (Primrose, 1976b) capable of producing C_2H_4. Arshad and Frankenberger (1989) reported that the corn rhizosphere was quite rich in microflora capable of synthesizing C_2H_4 from L-methionine (L-MET). Soil microorganisms can produce C_2H_4 from a variety of substrates (Chou and Yang, 1973; Considine and Patching, 1975; Primrose, 1976a) in addition to L-MET, a physiological precursor of C_2H_4 in plants (Lieberman and Mapson, 1964). Various amino acids, organic acids, carbohydrates, proteins, alcohols, and vitamins typically reported in root exudates and MET analogs, stimulate C_2H_4 production in soil (Arshad and Frankenberger, 1990c).

Jackson and Campbell (1975) reported that C_2H_4 gas applied to roots in nutrient solution could move from roots to shoots and create a physiological response in plants. Arshad and Frankenberger (1988) demonstrated the direct effect of microbial produced C_2H_4 on etiolated pea seedlings which exhibited the classical "triple" response to L-MET-dependent C_2H_4 released as a microbial metabolite. This response was only observed in those treatments which included *Acremonium falciforme* as fungal inoculum and L-MET as an C_2H_4 substrate in the case of sterile soil (autoclaved) or when L-MET was applied to nonsterile soil. L-Methionine added to an autoclaved soil without an inoculum did not promote the "triple" response indicating that L-MET was metabolized to C_2H_4 outside the seedling roots by the inoculum or by the soil indigenous microflora.

Based upon these observations, glasshouse experiments were undertaken with the objective to evaluate the effect of pretested C_2H_4 precursors, L-MET and L-ethionine (L-ETH) applied to soil on the growth of corn and tomato, respectively.

Materials and methods

Ethylene biosynthesis in soil

Prior to initiating the glasshouse study, C_2H_4 production in soil amended with $1\,mg\,g^{-1}$ of L-MET or L-ETH was monitored over a period of 14 d of incubation under ambient conditions (24 ± 3 °C). For this purpose, 125-mL Erlenmeyer flasks containing 50 g of Handford soil (coarse-loamy, mixed, nonacid, thermic Typic Xerorthent), capped with Mininert valves (Pierce, Rockford, IL) were used. Both substrates were added as solutions with the soil being maintained at field capacity (-33 kPa). A control received equivalent amounts of water. This experiment was carried out in triplicate and C_2H_4 concentrations were determined by gas chromatography by withdrawing 1-cm^3 gas samples from the head space above the soil with a gas-tight glass hypodermic syringe. The gas chromatograph (Varian Model 2700) was equipped with a flame-ionization detector (FID) and a 6 ft Porapak N(80—100 mesh) column. The column was operated isothermally at 80 °C. The operating conditions consisted of the following: sample size, 1 cm^3; carrier gas (N_2), $13\,mL\,min^{-1}$; H_2 flow, $30\,mL\,min^{-1}$; air flow, $300\,mL\,min^{-1}$;detector temperature, 200 °C; integrator, HP3390A. Peak area and retention times for C_2H_4 were compared to reference standards which were made by diluting 99.5% C_2H_4 obtained from Matheson (East Rutheford, NJ).

Glasshouse experiments

Seeds of *Zea mays* L. cultivars, Kandy Korn E.H. (Lot 6807-2, Burpee, Warminster, PA) and Miracle (Lot 6035-0, Burpee, Warminster, PA) and the tomato cultivar Bonny Best (3619, Tomato Growers Supply Co., Fort Myers, FL) were germinated in sand flats, to obtain uniform size of seedlings. The plants were then transferred to one-gallon pots containing 8.0 kg of sieved (2-mm) field moist Hanford soil having a pH of 6.1; total N, $1.06\,g\,kg^{-1}$; and total organic matter, $13.6\,g\,kg^{-1}$. To nutrify the soil and stabilize the indigenous microbial population, the soil was preconditioned 10 d prior to transplanting with one application of Hoagland mineral nutrient solution (one liter, full-strength). Seedlings of corn cultivars were transferred to the pots after 10 d and for tomato, 15 d after emergence. The seedlings were allowed to establish themselves prior to the application of the treatments. Mineral nutrient solutions were applied regularly throughout the experiments to eliminate nutritional stress. Data obtained on the growth and yield parameters were subjected to analysis of variance and comparison of means was made with Duncan's multiple range test.

Zea mays *L.*

This study was conducted during the months of August through October, 1988. Various concentrations of L-MET in solution (1.85×10^{-3} to 185.0 mg kg^{-1}) were applied to soil 10 d after transplanting as a one-time application. Controls received no L-MET. All treatments were run in replicates of eight. Plant growth was monitored over the vegetative growth of corn and harvested at the onset of tasselling (51 d after emergence). Shoot height was measured between the sixth node (near the soil surface) and the uppermost visible leaf collar, with weekly measurements throughout the experiment. Stem diameter at the ninth node was determined using a Digimatic Caliper (Mituyo 500, Tokyo, Japan). Internodal distance was measured between the eighth and ninth nodes. Leaf width was measured at the mid-point of the leaf originating from the ninth node of every plant. Relative resistance of stem breaking was measured between the eighth and ninth nodes by using an apparatus shown in Figure 1. This electrically operated instrument consisted of a dial indicating the force required to bend the corn stalk to a specified angle. After recording the shoot fresh weight, root and shoot dry weight was measured following drying at 65 °C for 48 h.

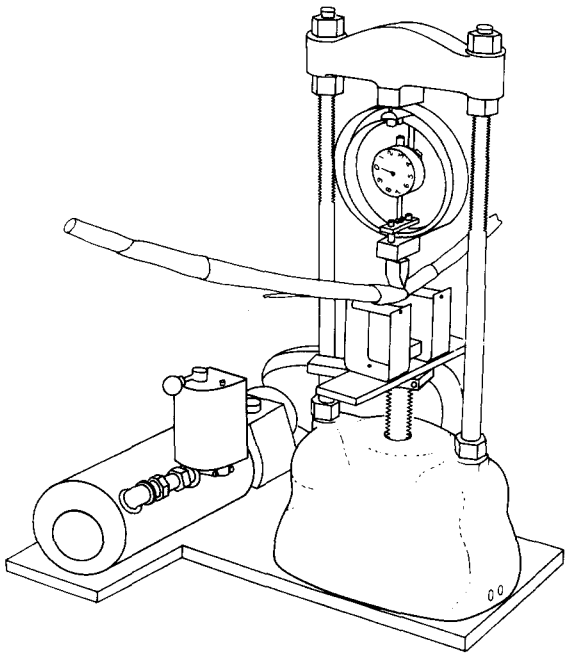

Fig. 1. Apparatus used to measure the relative resistance of corn to stem breaking.

Lycopersicon esculentum

This study was carried out during the months of August through December, 1988. L-Ethionine, another excellent substrate for C_2H_4 biosynthesis in soil, was applied in concentrations ranging from 2.0×10^{-4} to 60.0 mg kg^{-1} 25 d after transplanting as a single dose. Controls received no L-ETH. All treatments were run in replicates of six. Epinasty was measured with a transparent protractor as an increase in the angle between the adaxial surface of a petiole (leaf 2 or 3) and the stem at 72 h after treatment. Fruit yield and ripening (degreening) were monitored throughout the experiment. Shoot and root dry weight were obtained by drying at 65 °C for 48 h.

Results

Both the amendments, L-MET and L-ETH, stimulated C_2H_4 production in soil to a much greater degree (299- and 313-fold, respectively) than the control during 14 d of incubation (Fig. 2). L-Methionine and L-ETH were comparable in their effectiveness as C_2H_4 precursors. This substrate-dependent C_2H_4 production in soil continued beyond 14 d which allowed sufficient time for exposure to the plant roots. Previous studies have shown that C_2H_4 concentrations as low as 1 nmole L^{-1} can evoke a plant response (Arshad and Frankenberger, 1988).

Zea mays *L.*

Overall, Kandy Korn showed a more pronounced response to L-MET compared to the Miracle cultivar (Tables 1 and 2). One interesting feature observed in this study was the decrease in shoot height compared to the control during the early stages of growth (14 d after treatment) in the case of plants receiving the highest dose of L-MET (185 mg kg^{-1} soil) (Fig.3). However, after 28 d, plants recovered from this depressing effect, and became taller than the control. Another consistent

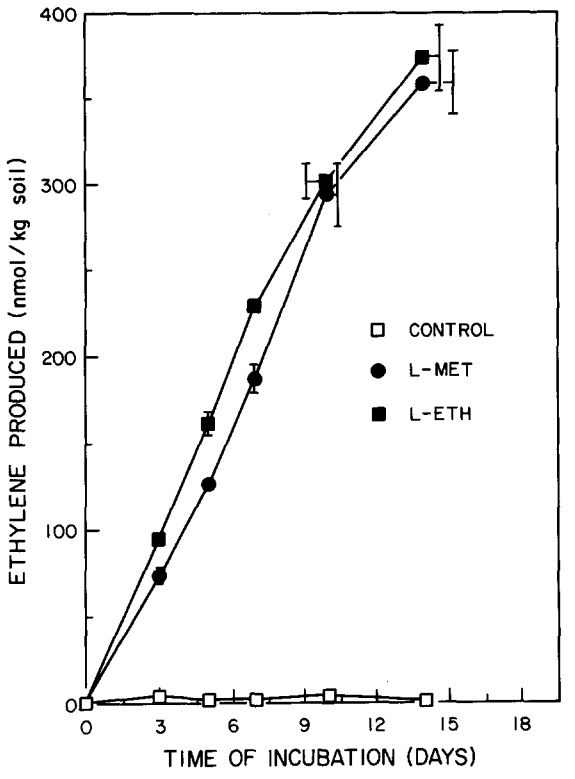

Fig. 2. Ethylene production in L-methionine and L-ethionine amended soil.

feature was that L-MET applied at 1.85 mg kg^{-1} resulted in the tallest shoots for both corn varieties (Fig. 3, Tables 1 and 2).

Analysis of variance and comparison of means according to Duncan's multiple range test revealed that all the growth parameters of Kandy Korn including shoot height, shoot fresh weight, shoot and root dry weight, internodal distance, stem diameter, uppermost leaf collar base distance, leaf width, and resistance to stem breaking were influenced significantly by L-MET treatments (Table 1). An L-MET treatment of 1.85 mg kg^{-1} gave the largest and significant increase in all the above-mentioned growth parameters compared with the control. L-Methionine concentrations $\leqslant$ 18.5 mg kg^{-1} significantly enhanced shoot height and concentrations ranging between 1.85×10^{-1} and 18.5 mg kg^{-1} promoted the shoot fresh weight over the control significantly. All the L-MET treatments tested showed a significant positive effect on internodal length and uppermost leaf collar base distance, compared with the control.

In the case of the Miracle cultivar, shoot height, shoot fresh weight, internodal length, stem diameter and resistance against stem breaking were significantly affected by L-MET applications while

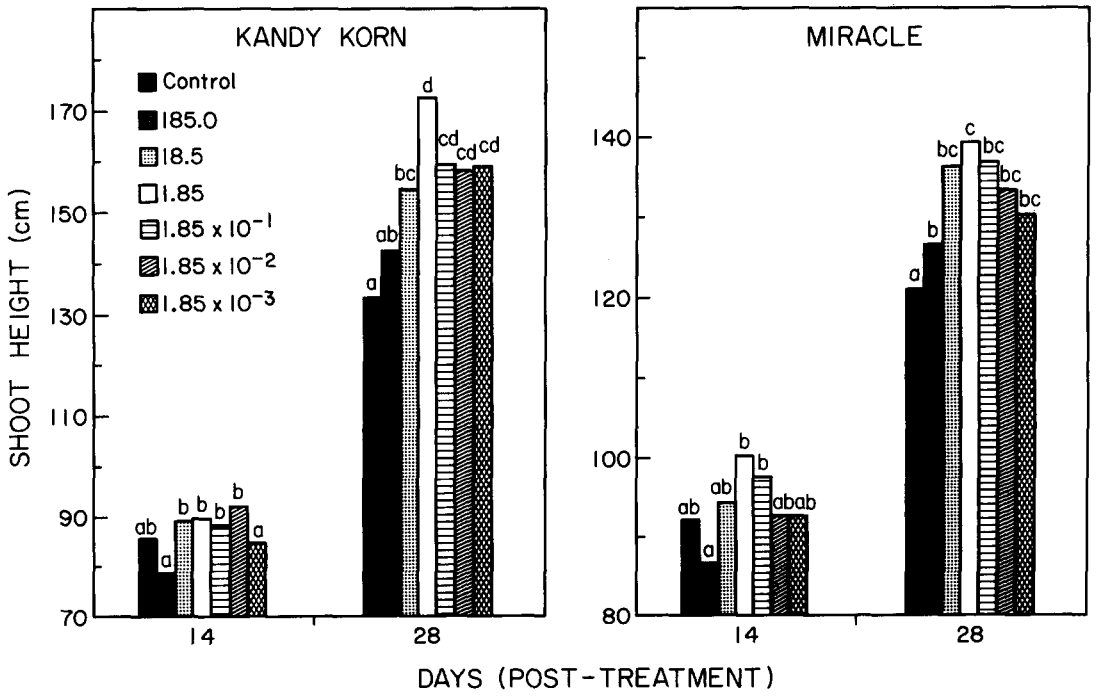

Fig. 3. Influence of L-methionine on shoot height of two corn cultivars at 14 and 28 days after treatment.

Table 1. Growth parameters of Kandy Korn as influenced by L-methionine applied to soil (average of 8 replicates)

L-Methionine ($mg\,kg^{-1}$)	Shoot height (cm)	Shoot fresh wt (g)	Shoot dry wt (g)	Root dry wt (g)	Internodal distance (cm)	Stem diameter (mm)	Uppermost leaf collar base distance (cm)	Leaf width (cm)	Resistance to stem breaking (relative units)
Control	134 a[a]	159 a	26.1 a	4.09 a	9.1 a	15.4 a	71.7 a	6.22 a	3.41 a
185.0	143 ab	176 a	26.7 a	4.14 a	11.6 b	16.8 ab	88.1 b	7.00 bc	3.66 ab
18.5	155 bc	195 bc	29.9 ab	4.57 ab	13.1 bc	16.9 ab	97.3 bc	6.75 abc	3.77 ab
1.85	173 d	231 d	34.5 b	5.35 c	14.6 c	17.4 b	112.4 c	7.35 c	4.35 b
1.85×10^{-1}	160 cd	206 cd	31.8 ab	4.86 bc	12.6 b	17.0 ab	112.4 c	7.11 bc	3.66 ab
1.85×10^{-2}	159 cd	185 abc	28.7 ab	4.25 a	11.5 b	16.7 ab	105.4 c	6.61 ab	3.67 ab
1.85×10^{-3}	160 cd	188 bc	30.8 ab	4.38 ab	11.6 b	16.9 ab	107.0 c	6.78 abc	3.67 ab

[a] Values followed by the same letter are not significantly different at the 0.05 level according to Duncan's multiple range test.

Table 2. Growth parameters of Miracle corn as influenced by L-methionine applied to soil (average of 8 replicates)

L-Methionine ($mg\,kg^{-1}$)	Shoot height (cm)	Shoot fresh wt (g)	Shoot dry wt (g)	Root dry wt (g)	Internodal distance (cm)	Stem diameter (cm)	Uppermost leaf collar base distance (cm)	Leaf width (cm)	Resistance to stem breaking (relative units)
Control	121 a[a]	221 a	33.2 a	5.49 a	7.8 a	18.6 ab	76.4 a	7.27 a	5.30 b
185.0	127 b	232 ab	31.4 a	5.51 a	9.7 a	19.7 cd	78.5 a	7.77 a	4.44 ab
18.5	136 bc	253 ab	30.4 a	5.54 a	10.1 b	20.0 cd	85.0 a	7.35 a	4.36 ab
1.85	140 c	258 b	32.3 a	5.89 a	10.4 b	20.1 d	84.9 a	7.23 a	4.35 ab
1.85×10^{-1}	137 bc	230 ab	30.5 a	5.60 a	11.1 b	19.1 abc	81.1 a	7.27 a	3.43 a
1.85×10^{-2}	134 bc	226 a	30.4 a	5.55 a	10.7 b	18.4 a	81.9 a	7.17 a	3.41 a
1.85×10^{-3}	131 bc	235 ab	31.2 a	5.40 a	10.0 b	18.9 abc	76.0 a	7.63 a	3.46 a

[a] Values followed by the same letter are not significantly different at the 0.05 level according to Duncan's multiple range test.

all other growth parameters remained unaffected (Table 2). An L-MET treatment of $1.85\,mg\,kg^{-1}$ was found to be the most effective for a maximum and significant enhancement of shoot height, shoot fresh weight and stem diameter, but contrary to the Kandy Korn, resistance against stem breaking was reduced by all the L-MET treatments compared to the control. All L-MET applications significantly promoted shoot height and internodal lenght, while fresh shoot weight was only significantly affected by the $1.85\,mg\,kg^{-1}$ application rate.

Lycopersicon esculentum

Epinasty in tomato plant leaves is a characteristic effect of C_2H_4 exposure. Table 3 illustrates the effect of L-ETH (as an C_2H_4 precursor added to soil) on the epinastic response of tomato. It is evident that all the treatments caused epinasty which differed significantly from that of the control. The maximum response in the second leaf was observed with the highest L-ETH dose ($60\,mg\,kg^{-1}$ soil) and in the third leaf, with a treatment of $20\,mg$ L-ETH kg^{-1}. Table 3 also shows the influence of L-ETH on shoot and root dry weight, fresh fruit yield, number of fruits, average weight of fresh fruit, number of ripe fruit, and percentage of total fruit ripened. It was observed that an application of L-ETH at $60\,mg\,kg^{-1}$ (maximum dose) initially depressed plant growth but later recovered after two weeks of application. Analysis of variance and comparison of means by Duncan's multiple range test revealed a significant effect of L-ETH on all the mentioned growth parameters except root dry weight. The data reveals that the lowest applied rate of L-ETH ($2.0 \times 10^{-4}\,mg\,kg^{-1}$) resulted in maximum shoot dry weight but gave the lowest yield in fresh fruit. The maximum fresh fruit yield was found with $0.2\,mg\,kg^{-1}$. The greatest number

Table 3. Growth parameters of Bonny Best tomato as influenced by L-ethionine applied to soil (aver age of 6 replicates)

L-Ethionine ($mg\,kg^{-1}$)	Epinastic movement (degrees) 72 h after treatment		Shoot dry wt (g)	Root dry wt (g)	Fresh fruit yield (g)	No. of fruits	Avg. wt of fresh fruit (g)	No. of ripe fruit[a]	
	Second leaf	Third leaf							
Control	3.3 a	4.8 a	106.7 ab	4.73 a	261 ab	7.00 ab	37.3 ab	1.83(23.8)[c]	ab
60.0	15.6 e	11.5 bc	104.4 ab	4.01 a	229 ab	4.83 a	47.5 abc	0.33(6.8)	a
20.0	11.6 de	12.3 c	93.7 a	4.59 a	351 abc	6.85 ab	50.1 abc	3.17(45.2)	c
2.0	10.2 bcd	9.8 b	107.9 ab	4.53 a	445 bc	7.16 ab	62.1 c	2.67(32.6)	bc
2.0×10^{-1}	10.1 cd	9.0 b	93 8 a	4.71 a	477 c	8.69 ab	55.0 bc	2.50(32.6)	bc
2.0×10^{-2}	8.6 bcd	9.6 bc	95.0 a	4.79 a	358 abc	9.33 b	38.4 ab	2.33(28.5)	bc
2.0×10^{-3}	7.1 b	7.5 b	104.9 ab	4.44 a	296 abc	8.17 ab	36.2 ab	2.17(26.5)	abc
2.0×10^{-4}	8.1 bc	8.0 b	111.2 b	4.69 a	209 a	6.00 ab	34.9 a	1.17(19.4)	ab

[a] Ripe fruit included breaker, pink, light orange, orange, red-orange and red tomatoes.
[b] Values followed by the same letter are not significantly different at the 0.05 level according to Duncan's multiple range test.
[c] Figures in parentheses indicate percent of total fruit ripened [(no. ripe fruit)/(total fruit) × 100].

of fruits per plant was obtained with $0.02\,mg\,kg^{-1}$. The average weight of fresh fruit was greatest and significantly different from the control with the treatment $2.0\,mg\,kg^{-1}$. The application of L-ETH to soil was also found to promote early fruit yield compared to the control (Table 4). The onset of fruit formation was observed 27 d after treatment with L-ETH concentrations ranging from 0.002 to $2.0\,mg\,kg^{-1}$ while the control and plants treated with $60\,mg\,kg^{-1}$ began fruit formation only after 41 d. At this stage (41 d), the cumulative number of fruits per plant which received L-ETH in the range of 0.002 to $20.0\,mg\,kg^{-1}$ were 5.0 to 8.0-fold greater than the control. L-Ethionine applied to soil also affected the ripening of fruits (Table 4). It was observed that the fruit began to ripen as early as 50 d after treatment with 20 mg L-ETH kg^{-1}, while control plants required 15 more days. At this stage (65 d), plants subjected to 20 mg L-ETH kg^{-1} soil had 5.5-fold more ripe fruit compared with the control.

Discussion

Both L-MET and L-ETH were applied to soil as precursors of C_2H_4. L-Methionine has been identified as a substrate for C_2H_4 biosynthesis by microorganisms (Arshad and Frankenberger, 1988;1989) and plants (Lieberman and Mapson, 1964) but L-ETH has not been thoroughly investigated as an C_2H_4 precursor added to soil. Since attempts were made to prevent nutrient and water stress, the response of corn and tomato plants to the treatments of L-MET and L-ETH is most likely attributed to C_2H_4 synthesized by soil microorganisms, although plant utilization of these added substrates and stimulation of endogenous C_2H_4 synthesis cannot be ruled out. However, our previous study (Arshad and Frankenberger, 1988) clearly showed that L-MET application to sterile (autoclaved) soil had no effect on etiolated pea seedlings indicating the inability of seedling roots to utilize L-MET applied to soil. A plant response was observed only when L-MET was added to nonsterile soil, indicating that it was a microbial-mediated reaction. This premise is supported by the inability of *Xanthium pennsylvanicum* tissue to utilize L-MET and L-ETH as an C_2H_4 precursor (Satoh and Esashi, 1980). Moreover, Jackson and Campbell (1975) have successfully demonstrated the movement of radiolabelled C_2H_4 present in nutrient solution from roots to shoots of tomato plants showing an epinastic response. Epinasty and early ripening observed in our tomato experiments clearly indicates C_2H_4 involvement. Epinasty and ripening of fruit are well defined C_2H_4-inducing physiological characteristics (Reid, 1987; Yopp *et al.*, 1986). Substrate-dependent microbial biosynthesis of C_2H_4 in soil involves a slow and gradual release of C_2H_4 over a period of time (Fig. 2), hence roots may be exposed to this metabolite during critical stages of development.

Previous work has indicated that C_2H_4, among the plant hormones often acts as an inhibitor rather than a stimulator of plant growth, but its interac-

Table 4. Influence of L-ethionine applied to soil on fruit formation and ripening[a] of Bonny Best tomato

L-Ethionine ($mg\,kg^{-1}$)	Cumulative number of fruit harvested per treatment Days after treatment						Cumulative number of fruit ripened per treatment Days after treatment						
	27	34	41	48	53	67	50	54	56	60	63	65	67
Control	0	0	3	18	25	42	0	0	0	0	0	2	11
60.0	0	0	5	10	17	29	0	0	0	0	1	2	2
20.0	0	5	22	28	34	42	2	2	3	5	6	11	19
2.0	4	9	21	32	36	43	0	0	0	2	2	9	16
2.0×10^{-1}	3	7	23	31	37	52	1	1	1	5	7	9	15
2.0×10^{-2}	2	6	24	33	39	56	0	1	1	4	6	8	14
2.0×10^{-3}	2	6	15	25	29	49	0	1	1	2	3	6	13
2.0×10^{-4}	0	3	8	14	21	36	0	0	0	1	1	2	7

[a] Ripe fruit included breaker, pink, light orange, orange, red-orange and red tomatoes.

tion with other plant hormones particularly with auxins has recently been established (Philosoph-Hades *et al.*, 1989; Riov and Yang, 1989; Sagee *et al.*, 1989; Vendrell and Dominguez, 1989; Yang and Hoffman, 1984). Stimulation of plant growth as observed in the case of corn and increased fresh fruit yield in tomato might be due to this interaction. Hormones do not act alone but are often in conjunction with, or in opposition to each other such that final growth and development represents the net effect of a hormonal balance (Leopold, 1980). An exogenous supply of C_2H_4 may alter this balance. The increase in plant height of corn due to L-MET treatments might be in response to Type 3 cells which exhibit elongation upon exposure to C_2H_4 as explained by Osborne (1984). Similar results have been reported by Poovaiah and Leopold (1973) who observed stimulation of bluegrass stem growth on exposure to C_2H_4. Kende *et al.* (1984) found a 2- to 3-fold enhanced internodal elongation of non-submerged rice when exposed to 0.4 μl L^{-1} C_2H_4. An application of 1, 5, and 10 μL L^{-1} C_2H_4 increased the total length of etiolated rice seedlings by 17, 21 and 24%, respectively, compared with the control (Raskin and Kende, 1983). Ishizawa and Esashi (1984) reported that C_2H_4 promoted elongation of rice coleoptile reaching a maximum at a concentration of 3 μL L^{-1}.

The plant response is presumably governed by the rate of hormone uptake, the active concentration of the regulator in the rhizosphere and the modification of the plant's own pool of hormones due to the addition of exogenous supplies (Frankenberger and Fitzpatrick, 1984). At early stages of growth in corn and tomato, the depressing effect observed with the highest amount of L-MET and L-ETH applied (185 and 60 mg kg^{-1}, respectively) may be due to the inhibitory effect of high levels of C_2H_4 produced. The opposite response displayed by the two corn cultivars in resistance to stem breaking could be attributed to water relations of the plants, partitioning of photosynthates and lignin formation. For both cultivars, L-MET treatments decreased the percent dry matter and hence increased the water content compared to the control. Mansfield (1987) has thoroughly discussed the hormonal regulation of water balance in plants.

Although the uptake of L-MET and L-ETH by plants and their metabolism within the tissue may be one mechanism of action, the response of both corn and tomato may also be attributed to the involvement of substrate-dependent C_2H_4 released by the soil indigenous microflora and/or a change in the balance of rhizosphere microflora discouraging root pathogens. This is the first study reporting the positive effect in plant growth of L-MET on corn and L-ETH on tomato when applied to soil at the seedling stage.

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