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The Effect of Ethylene on Adventitious Root Formation in Mung Bean (*Vigna radiata*) Cuttings

J. A. Robbins,[1] M. S. Reid,[1] J. L. Paul,[1] and T. L. Rost[2]

[1]Departments of Environmental Horticulture and [2]Botany, University of California at Davis, Davis, California 95616

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Abstract. A promotive effect of ethylene on the formation of adventitious roots by mung bean cuttings was demonstrated using a recirculating solution culture system to apply dissolved ethylene. The number of roots increased in proportion to the length of exposure to the gas. Mean root numbers per cutting for a 4-day exposure to ethylene and an air control were 45 and 19, respectively. The tissue was most sensitive to a 24-h ethylene "pulse" 2–3 days after taking cuttings. Rooting was maximal at a concentration of 13 $\mu l\ l^{-1}$ ethylene. The ethylene treatment inhibited the growth of roots and terminal buds. Application of Ag^+, as silver thiosulfate, reversed the effect of ethylene on the two growth responses but had no effect on root numbers. Norbornadiene, another inhibitor of ethylene action, reversed all three ethylene responses.

Numerous workers have used the ethylene-releasing compound (2-chloroethyl) phosphonic acid (ethephon) to examine the effect of ethylene on the rooting of cuttings. Although the results of these studies have been quite variable (Geneve and Heuser 1983, Johnson and Hamilton 1977, Lipecki and Selwa 1973, Swanson 1976), most indicate that ethephon either promotes rooting (Carpenter 1975, Krishnamoorthy 1971, 1972, Robbins et al. 1983b, Roy et al. 1972) or has no influence on it (Chong 1982, Criley and Parvin 1979, Mudge and Swanson 1978, Nell and Sanderson 1972, Samananda et al. 1972, Sanderson and Patterson 1980, Schier 1975). This variable response to ethylene could be expected, as a large number of species at different stages of development have been tested under a range of experimental conditions. Furthermore, ethephon may have extraneous effects on rooting which make interpretation of results difficult. These effects include the acidity of unbuffered so-

lutions (Reid et al. 1980), the pH dependency of release rate (Mudge and Swanson 1978), and the possible influence of breakdown products on rooting results.

Relatively few workers have examined the effect of ethylene gas on rooting. Zimmerman and Hitchcock (1933) showed that ethylene promoted the growth of preformed roots in woody cuttings and induced adventitious root formation in intact plants. In contrast, Mullins (1972) found that over a wide range of concentrations (1–1000 $\mu l\ l^{-1}$) ethylene applied to stem segments from etiolated mung bean seedlings inhibited the formation of adventitious root primordia. Batten and Mullins (1978), using similar segments from mung bean, found no influence of the gas on rooting, although their results are difficult to evaluate because ethylene gas was applied in combination with auxin. To further study the effects of ethylene on adventitious root formation in leafy cuttings, a recirculating solution culture system was developed that allows dissolved ethylene gas to be applied to their stems (Robbins et al. 1983a).

We report here the effects of length of exposure, concentration, and time of application of ethylene gas on adventitious root formation in light-grown mung bean cuttings. The inhibitors of ethylene action, Ag^+ and 2,5-norbornadiene (bicyclo [2.2.1] hepta-2,5-diene) (Sisler and Goren 1981) and histological studies were used to examine how and at what developmental stage ethylene may be acting.

Materials and Methods

Mung bean (*Vigna radiata* (L.) R. Wilcz. "Berkin") seedlings were grown in vermiculite (95% of the particle sizes between 1 and 4 mm) in a growth chamber at a continuous temperature of 27°C and 65% relative humidity under a 16-h photoperiod with a photosynthetic photon flux density (PPFD) of 300 $\mu mol\ m^{-2}\ sec^{-1}$ (cool-white fluorescent tubes and incandescent bulbs). Plants were watered by a constant level system with half-strength Hoagland's solution (Hoagland and Arnon 1950).

Cutting Preparation and Rooting System

Cuttings 10–11 cm long were made from uniform 7-day-old seedlings. A cutting consisted of a terminal bud, two primary leaves, the epicotyl, and 3 cm of hypocotyl. Cuttings were treated with gas and rooted in the recirculating solution culture system previously described (Robbins et al. 1983a). The system comprised a 3.5-l solution reservoir, a pump, and a rooting module (12 rooting vessels each holding 5 cuttings) made from PVC pipe, Tygon tubing, and disposable syringe barrels. Rooting solution (9 $\mu M\ H_3BO_3$, 1 mM $CaCl_2$ in DI water) was pumped to the module at a flow rate of 420 ml min^{-1} (5 exchanges $vessel^{-1}\ min^{-1}$) and then returned to the reservoir. The hypocotyls were immersed in the rooting solution. Ethylene gas or ethylene-free air (passed through a $KMnO_4$ scrubber) was bubbled into the solution reservoir at 36 l h^{-1}. The mean number of visible roots was counted 5 days after the cuttings

were made. Because primordia emerge very quickly, a count of emerged roots is a good measure of the number of primordia. Results are reported as means of 12 vessels each containing five cuttings. Standard errors of the means are shown as perpendicular bars on each graph.

Environmental Conditions for Rooting

Experiments were carried out in a laboratory at a PPFD of 260 μmol m^{-2} sec^{-1} (cool-white fluorescent tubes), 55% relative humidity, 27/21°C day/night temperature. Studies investigating the effect of ethylene concentration and inhibitors of ethylene action on root formation were conducted under environmental conditions similar to those in which the plants were grown.

Ethylene Measurements

Ethylene concentration was measured using an analytical gas chromatograph (Carle, Anaheim, CA) equipped with a photoionization detector (HNU Systems, Newton, MA) coupled to a high-sensitivity electrometer (Keithley, Cleveland, OH) for measurement of low concentrations of ethylene. Gas samples (3 ml) were taken either from the gas lines leading into the solution reservoirs or near the foliage of cuttings. Ethylene levels were monitored twice daily. Background levels measured near the foliage never exceeded 30 nl l^{-1}. These low background levels are possible even when bubbling high concentrations of ethylene, as the module design acts to draw outside air into the rooting vessel, minimizing foliar exposure to ethylene. Although ethylene is rather insoluble in water, the fast bubbling rate of gas into the solution reservoir and rapid transport of solution to the rooting vessels compensated for outgassing and allowed the system to reach equilibrium within a few minutes. The ethylene contents of samples of solution taken from the solution reservoir and from the rooting vessels were the same.

Length of Exposure to Ethylene

Using five individual rooting systems, 6 μl l^{-1} ethylene gas was applied continuously for either 1, 2, 3, or 4 days. Following ethylene application, ethylene-free air was bubbled into solution for the remainder of the gassing period (up to 4 days). The control (0 day) treatment was a 4-day application of ethylene-free air.

After counting emerged roots, several cuttings were cleared for 24 h in a solution of 20 g l^{-1} NaOH containing 0.1 ml l^{-1} Johansen's Safranin and the primordia inside the cutting were counted under a stereomicroscope. The number of these unemerged primordia never exceeded one or two per cutting.

To identify the stages of root formation in both ethylene (6 μl l^{-1}) and air-treated cuttings, one plant was selected at random from each treatment for anatomical analysis starting on day 0 (a seedling) through day 4. Thin free-

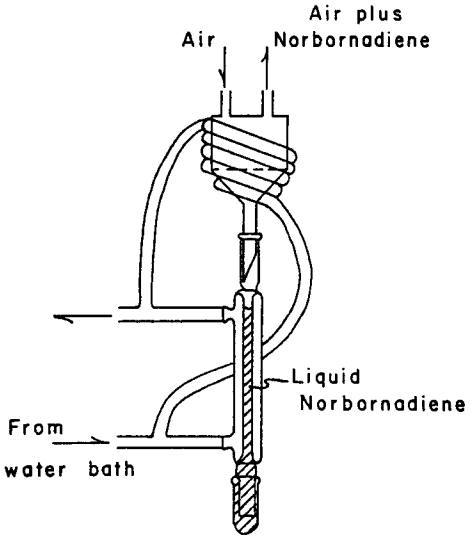

Fig. 1. Unit used for the continuous volatilization of norbornadiene. The volatilization unit is composed of a Liebig condenser, Büchner funnel, and cap with gas ports. Volatilization is accomplished by passing heated water through the condenser and the tubing wrapped around the Büchner funnel.

hand sections were taken at a point 2.75 cm below the cotyledonary node (0.25 cm above the base of a cutting). Sections were stained with 0.05% toluidine blue and then viewed under a stereomicroscope.

Ag^+ Experiments

The anionic silver thiosulfate complex (STS) was used as an inhibitor of ethylene action (Veen 1983). Prepared cuttings were dipped for 15 min in shell vials containing 10 ml (solution covered the entire hypocotyl) of either DI water or a 1-mM STS solution. Following treatment, cuttings were rinsed in DI water and placed into the rooting system for further treatment with solutions equilibrated with either ethylene or ethylene-free air. After 5 days, visible roots were counted, and buds and emerged roots were excised for fresh and dry weight (70°C, 24 h) measurements.

Norbornadiene Experiments

Norbornadiene, although a liquid at room temperature, was applied to cuttings in a manner similar to that used for ethylene. Norbornadiene was continuously volatilized into the air stream in a system (Fig. 1) comprising a Liebig condenser, Büchner funnel, and cap with gas ports. Changing the temperature of the water passing through the condenser and the tubing wrapped around the Büchner funnel altered the concentration of norbornadiene gas in the exit air stream.

Norbornadiene levels were measured with a gas chromatograph (Varian, Palo Alto, CA) equipped with a column of 10% Carbowax 400 on Chromosorb W-HP (80/100 mesh) and a flame ionization detector. Gas samples (10 μl) were taken either from the gas lines leading into the solution reservoirs or near the

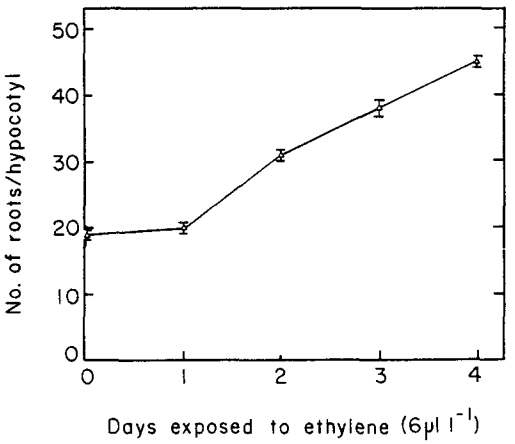

Fig. 2. The relationship between length of continuous exposure to ethylene and number of visible roots in mung bean hypocotyls. Following the ethylene treatment, hypocotyls were exposed to ethylene-free air. Control treatment (0 day) consisted of a 4-day exposure to ethylene-free air. Each point represents the mean and SE for 60 cuttings.

foliage of cuttings. No detectable levels of norbornadiene were found near the foliage of cuttings.

24-Hour Ethylene "Pulse" Experiment

A pulse experiment was performed to determine which developmental stage was most affected by ethylene. A single 24-h pulse of ethylene (6 µl l^{-1}) was applied during day 1, 2, 3, or 4 after cuttings were made. When cuttings were not exposed to ethylene, ethylene-free air was bubbled into the solution.

Ethylene Concentration Experiment

To determine the effect of ethylene concentration on rooting, five rooting systems were used, each having a different concentration of ethylene bubbled into it for 96 h. Concentrations were 6, 26, 50, and 110 µl l^{-1} in the first experiment and 6, 13, 25, and 36 µl l^{-1} in the second. Controls were exposed for 96 h to ethylene-free solution.

Results

Length of Exposure to Ethylene

Between 1 and 4 days the number of adventitious roots increased in proportion to the length of exposure to 6 µl l ethylene (Fig. 2). Numbers of roots per cutting in the control and 4-day exposure samples were 19 and 45, respectively. The distribution of roots was different in control and ethylene treated cuttings. Roots in control cuttings were all basal, whereas those of ethylene-treated cuttings were distributed over the entire hypocotyl section, with root density increasing toward the basal end. Ethylene also affected root morphology. Roots

Table 1. The effect of a 15-min STS (1 mM) pulse and a 4-day exposure to ethylene (6 μl l^{-1}) or ethylene-free air on dry weight/bud, dry weight/root, or the number of roots/hypocotyl.

Treatment	Dry weight (mg)[a]		Number of roots/hypocotyl[a]
	Bud	Root	
Air	2.6 b	0.24 b	18 a
Ethylene	1.8 a	0.15 a	29 c
STS/ethylene	3.2 c	0.22 b	27 b
STS	3.7 c	0.26 b	19 a

[a] Means (60 cuttings/treatment) within a column followed by the same letter are not significantly different according to Duncan's Multiple Range Test ($p = 0.05$).

exposed to ethylene during days 3 and 4 were shorter and developed more root hairs than air controls, and sometimes became ageotropic.

Thin free-hand sections removed daily from both ethylene and air-treated cuttings showed the following gross anatomical features: no observable primordia on day 0; nuclei of phloem parenchyma cells enlarged and darkly stained on day 1; definite organization of cells into a conical mass with no vascular connections on day 2; primordia enlarged, disrupting the cortex and epidermis, several emerged on day 3; and all roots emerged on day 4. Root primordia develop from phloem parenchyma cells of the four major vascular bundles. Developmental stages observed correspond well with those described in detail by Blazich and Heuser (1979). No difference in the timing of stages or appearance of cells was observed between the ethylene-treated and control tissues. These stages were observed at a distance 2.75 cm down from the cotyledonary node; development above this point would be slightly delayed.

Ag^+ and Norbornadiene Treatment

The increase in root number in ethylene treatments was also accompanied by a decrease in the dry weight of individual buds and roots (Table 1). Increasing either the length of exposure or the concentration of ethylene decreased individual root and bud dry weight proportionately.

When cuttings were treated with STS and then ethylene, two of the three ethylene responses were eliminated (Table 1). Silver thiosulfate restored the growth of both buds and roots to that of the control but had no effect on ethylene-stimulated rooting. Bud dry weight in silver-treated cuttings increased more than that of buds from the air control cuttings.

Norbornadiene (7000 μl l^{-1}) partially reversed ethylene's effect on bud and root growth (Table 2) and completely inhibited ethylene's effect on root number. Norbornadiene alone increased root growth and decreased root number of the air controls. Norbornadiene also reversed ethylene's effect on root hair production and geotropism (data not shown).

24-Hour "Pulse"

At 27°C, application of ethylene as a single 24-h pulse on days 1–4 resulted in maximal stimulation of root numbers when the gas was applied during the

Table 2. The effect of a 4-day exposure to norbornadiene (7000 μl l^{-1}) and/or ethylene (6 μl l^{-1}) on dry weight/bud, dry weight/root, or the number of roots/hypocotyl.

Treatment	Dry weight (mg)[a]		Number of roots/hypocotyl[a]
	Bud	Root	
Air	1.8 a	0.25 b	22 b
Ethylene	0.8 b	0.12 d	40 a
Norbornadiene/ethylene	1.1 b	0.20 c	22 b
Norbornadiene	1.5 a	0.31 a	16 c

[a] Means (60 cuttings/treatment) within a column followed by the same letter are not significantly different according to Duncan's Multiple Range Test ($p = 0.05$).

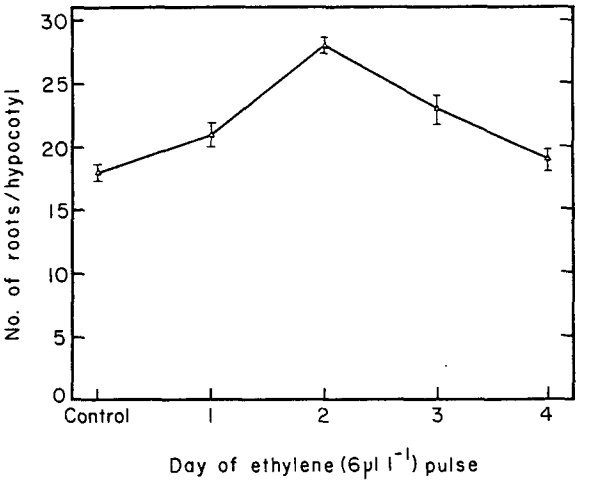

Fig. 3. The effect of single 24-h ethylene pulses applied at different times on the number of visible roots in mung bean hypocotyls. When not exposed to ethylene, hypocotyls were treated with ethylene-free air. Controls were exposed for 4 days to ethylene-free air. Means ± SE of 60 replicate cuttings.

second 24-h period (Fig. 3). The number of roots was counted on day 5 of the experiment, regardless of the day of ethylene application. The length of time between the application of ethylene and the evaluation of rooting results was therefore not equal for all treatments.

A separate experiment (data not shown) was conducted comparing the results obtained when an equal period elapsed between the ethylene application and rooting evaluations, and those obtained when rooting evaluations were conducted on day 5 for all treatments. For a given day of ethylene application, equivalent results were obtained regardless of the day of evaluation. Free-hand sections taken from cuttings given an ethylene pulse during the second 24-h period revealed that primordia were well formed at this time. When the experiment was repeated at 21°C, maximal rooting was obtained on day 3 (data not shown).

Ethylene Concentration

Adventitious root initiation was found to be responsive to ethylene concentration (Fig. 4). Because of the limited resolution of the first experiment, a second experiment was performed to obtain a better estimate of the optimum concen-

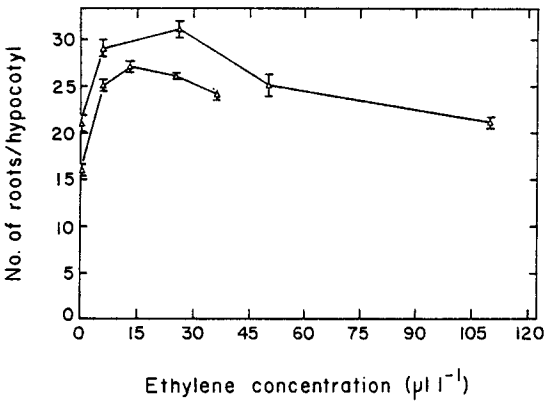

Fig. 4. The relationship between number of visible roots in mung bean hypocotyls and ethylene concentration (4-day exposure). Each point represents the mean and SE for 60 cuttings. The curves are from separate experiments.

tration for rooting. The maximum response in the second experiment occurred at 13 μl l^{-1}. Roots were measurably shorter, produced more root hairs, and were somewhat ageotropic when the concentration was greater than 50 μl l^{-1}.

Discussion

The data presented here demonstrate clearly that application of ethylene gas to the hypocotyls of leafy mung bean cuttings significantly increases the number of adventitious roots. This increase results primarily from development of more roots distal to the cut end. The response to ethylene was maximal at approximately 13 μl l^{-1} (Fig. 4), a concentration close to the saturation level (10 μl l^{-1}) reported for many other plant responses (Abeles 1973). In contrast to many other ethylene responses, the effect of ethylene decreased at higher concentrations. A 4-day exposure to 110 μl l^{-1} ethylene did not stimulate rooting (Fig. 4), perhaps because higher ethylene concentrations increased the activity of other processes that inhibit rooting.

The number of roots increased in proportion to the time of continuous exposure to ethylene up to 4 days (Fig. 2). This is also markedly different from most ethylene responses, which typically require exposure for less than 24 h (Abeles 1973). Results from an experiment where ethylene was applied as single 24-h pulses indicate a differential responsiveness by mung bean cuttings to ethylene (Fig. 3). One possible explanation for this response is the temporal changes in the auxin gradient in the hypocotyl. Following the taking of a cutting, auxin accumulates at the base of the cutting (Weigel et al. 1984, Greenwood and Goldsmith 1970, Baadsmand and Andersen 1984, Friedman et al. 1979). Additional auxin can accumulate above this point as a result of an inhibition of auxin transport by ethylene (Morgan and Gausman 1966). Increasing the length of exposure to ethylene would increase the auxin concentration at points even higher in the cutting. Toward the end of the second day following the taking of a mung bean cutting, the basally accumulated auxin begins to diminish as the new root system forms (Weigel et al. 1984). Therefore, maximal rooting occurs in response to an ethylene pulse during day 2 because

the accumulated auxin is at its peak, so that ethylene application results in the highest possible auxin concentration in the upper part of the hypocotyl.

Exogenous application of 6 $\mu l\ l^{-1}$ ethylene during the first 24 h (Fig. 3) or of a wide range of other concentrations during the first 12 h (data not shown) had no effect on final root numbers. This may not, however, indicate that ethylene is not involved in root development at this time. The wounding of the tissue implicit in taking the cutting undoubtedly stimulates a transitory production of ethylene (Yang and Pratt 1978), which may be adequate to stimulate initials present at that time.

The time from taking the cutting to the emergence of the first visible roots in mung bean cuttings is 3 days, and there were very few stainable primordia remaining when the root count was made on day 5. It is surprising that continued application of ethylene during day 4 further increased root numbers (Fig. 2), since only 1 day remained for the emergence of these additional roots following the ethylene treatment. It would appear that late ethylene treatment stimulated the growth of initials that had already developed to a stage immediately preceding stainable primordia.

Robbins et al. (1983b) found that ethephon applications stimulated rooting in mung bean. The data reported here show that this response was truly an ethylene effect and not simply an artifact of ethephon. The results of other workers who have examined the response of cuttings to ethylene or ethephon have been variable. Our data indicate that the concentration (Fig. 4), length (Fig. 2), and time (Fig. 3) of ethylene application can influence rooting results and may account for some of this variability. It is possible that the promotive effect of ethylene on rooting may require the presence of buds and leaves (Batten and Mullins 1978), the primary source for auxin.

While continuous ethylene treatment enhanced root numbers, it reduced growth of the roots and the apical bud (Table 1). These data appear to suggest that ethylene is acting by changing the relative sink strength of the apical bud and the root initials. When the cuttings were pretreated with STS, however, the growth of roots and bud was restored without reduction in root numbers, indicating that nutrients were not limiting. The application of Ag^+ as the STS complex inhibits a wide variety of ethylene responses (Veen 1983). Its failure to inhibit the rooting response is a curious and as yet unexplained exception. It seems possible that the silver from the pulse treatment used in these experiments did not penetrate to the site of root initiation. The ability of norbornadiene to reverse all three responses (Table 2) supports this hypothesis.

A reduction in root number on cuttings treated with norbornadiene alone (Table 2) suggests that endogenous ethylene may play an important role in adventitious root formation. The idea that low levels of endogenous ethylene contribute to "normal" rooting is further substantiated by the observed effect of an inhibitor of ethylene synthesis (aminoethoxyvinylglycine—AVG) on rooting of mung bean cuttings (Robbins et al. 1983b). Cuttings exposed for 24 h to 10 μM AVG produced 39% fewer roots; a 6-day exposure almost totally inhibited rooting.

An alternative explanation for the decreased root number of cuttings treated with norbornadiene is that norbornadiene is toxic to the rooting response. However, the lack of any effects on bud and root growth (Table 2), or on the

color or length of roots, and the absence of phytotoxic symptoms suggest that at the concentration used in these experiments norbornadiene was not toxic.

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