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Herbicidal Actions of Root-Applied Glufosinate Ammonium on Tomato Plants

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Abstract. The herbicidal action of foliar applications of glufosinate-ammonium (GLA) is due to toxic accumulation of unassimilated NH_4^+ in leaves; however, the effects of root-applied GLA on NH_4^+ accumulation and plant growth are unknown. In a dose-response hydroponics experiment, tomato (*Lycopersicon esculentum* Mill.) plants were grown in nitrate-based solutions with GLA added at 0, 6, 12, 25, or 50 mg·L^{-1}. To observe plant responses to an exogenous NH_4^+ source with herbicide-induced responses, plants were grown in an NH_4^+-based solution without GLA addition. At 6 days after treatment (DAT), GLA in solution at 25 mg·L^{-1} produced partial leaf wilting, chlorosis, and necrosis of foliage, and at 50 mg·L^{-1}, plants were fully wilted and necrotic. Ammonium (NH_4^+-N) concentration in shoots at 6 DAT increased from 0 to 6 mg·g^{-1} fresh weight with increasing GLA in the nutrient solution. Ethylene evolution doubled (from 4 to 8 nL·g^{-1}·h^{-1}, fresh weight) with increases in GLA from 0 to 25 mg·L^{-1} but declined with apparent plant death with GLA at 50 mg·L^{-1}. Other treatments, including NH_4^+ nutrition, did not induce toxicity symptoms in leaves or give increases in NH_4^+ accumulation or ethylene evolution during the 6 days of the experiment. In a time-course experiment, tomato plants treated with GLA at 25 mg·L^{-1} were chlorotic at 4 DAT. Ethylene evolution (fresh weight basis) rose from an initial rate of 2.6 nL·g^{-1}·h^{-1} to 8.3 nL·g^{-1}·h^{-1} after 4 days. At 9 DAT, all plants receiving this treatment died. In the time-course experiment, an exogenous NH_4^+ treatment caused a slight inhibition in shoot fresh weight relative to NO_3^- nutrition with no GLA but caused no visible symptoms and only slight enhancements in NH_4^+ accumulation and ethylene evolution over the 9-day period. Following GLA treatment, NH_4^+ accumulated in the shoots and increased sharply with time, whereas exogenous NH_4^+ led to NH_4^+ accumulation primarily in roots. Results suggest that GLA was absorbed by roots and translocated to shoots, where it initiated accumulation of NH_4^+ and ethylene evolution as indications of herbicidal action. Chemical name used: glufosinate-ammonium, GLA.

Glufosinate-ammonium (GLA) is a postemergence herbicide that produces phytotoxic effects by inhibiting glutamine synthetase (GS) in chloroplasts, thereby blocking synthesis of glutamine from glutamate and thus assimilation of NH_4^+ (Manderscheid and Wild, 1986). This inhibition results in NH_4^+ accumulation and ultimately in plant death (Koecher, 1983; Krieg et al., 1990; Leemans et al., 1987; Manderscheid and Wild, 1986; Tachibana et al., 1986; Wild et al., 1987). Increases in NH_4^+ concentrations in shoots are a rapid and sensitive indicator of inhibition of GS (Mersey et al., 1990). Sources of cellular NH_4^+ accumulation include NO_3^- reduction, catabolism of organic N compounds, and glycine to serine conversion during photorespiration (Joy, 1988; Wild et al., 1987). Ethylene evolution is a response of plants to NH_4^+ toxicity and other physiological stresses (Feng and Barker, 1992) and hence may be an indicator of GLA action.

Glufosinate-ammonium is used as a foliar spray at concentrations between 100 and 500 mg·L^{-1}. As a nonselective herbicide, GLA has been used in minimum tillage systems, in orchards and vineyards, and in chemical fallowing and as a preharvest desiccant (Stechel et al., 1997). Its relatively short half-life in soils, 6 to 23 d, is assumed as an indication of GLA safety (Hoerlein, 1994). However, consideration should be given to the potential of GLA remaining active for longer than the stated half-life in coarse-textured soils. Another consideration is that accumulation in plants may be herbicidal to crops, following GLA transport in soil and absorption through roots. Therefore, the current research studied the effects of root application of GLA on tomato plant growth, NH_4^+ accumulation, and ethylene evolution. Tomato was chosen for its sensitivity and documented responses to NH_4^+ toxicity (Barker et al., 1967).

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Materials and Methods

Plant material and general procedures. This study was conducted with hydroponics in a greenhouse. Tomato seeds ('Heinz 1439') were germinated in 1 peat : 1 vermiculite (v:v) medium. One week after germination, seedlings were transplanted to 1.5-L opaque plastic containers filled with half-strength, NO_3^--based solution (Hoagland No.1, Hoagland and Arnon, 1950) to preculture for 1 week. Two experiments were conducted to assess the effects of root-applied GLA (monoammonium-2-amino-4-hydroxy(methyl) phosphinyl butanoate; trade name, Finale, 11.33%, w/v, a.i., Hoechst Schering AgrEvo, Somerville, N.J.). A dose experiment assessed plant responses to increasing concentrations of GLA in a given time period, and a time-course experiment assessed the effects of duration of plant exposure to a herbicidal level of GLA. Each treatment was replicated in three randomized complete blocks in a greenhouse under ambient conditions of temperature (≈18 °C day and night) and light (≈800 μmol·m^{-2}·s^{-1}) in spring 1998. Effects of treatments were assessed by analysis of variance, regression, and by standard deviations (Steel and Torrie, 1980).

Dose experiment. In full-strength, NO_3^--based (Hoagland No. 1) solution (self-stabilized at pH 7.0 during plant growth), GLA was added to a final active ingredient concentration of 0, 6, 12, 25, or 50 mg·L^{-1}. These concentrations were chosen after a preliminary experiment determined concentrations at which effects of GLA ranged from none to plant death (total wilting and necrosis of foliage) over a 7-d period. In another treatment, tomato plants received NH_4^+ at 210 mg N/L from an NH_4^+-based, modified Hoagland solution (Maynard and Barker, 1969) with no GLA and at a self-stabilized pH 4.5. Containers were checked daily and refilled with nutrition solutions as needed without further GLA additions. At 6 d after treatment, NH_4^+ toxicity symptoms appeared, and plants from all treatments were harvested for ethylene, NH_4^+ (see below), and biomass (fresh weight of shoots and roots) determinations.

Time-course experiment. In this experiment, tomato plants were treated with GLA at 25 mg·L^{-1}, which was chosen because it was effective without causing plant death in 6 d in the dose-response experiment. The treatment with externally supplied NH_4^+ was included as above. Entire roots and shoots for biomass and samples for NH_4^+ determinations (see below) were taken every 1 or 2 d from the first day of treatment until plant death from herbicide treatment.

Ethylene analysis (both experiments). Terminal portions of tomato shoots including the first fully expanded leaf (≈10 g fresh weight in each sample) were removed for determinations of ethylene evolution (or NH_4^+, see below). The tips were placed in 500-mL canning jars, which were sealed with serum caps inserted in the lids. After 2 hours, ethylene concentration in the jars was measured by taking 2-mL portions from the jars for analysis by gas chromatography (column GDX-502, mesh 60 to 80, set at 150 °C, N_2 carrier gas, and flame ionization detector) (Feng and Barker, 1992).

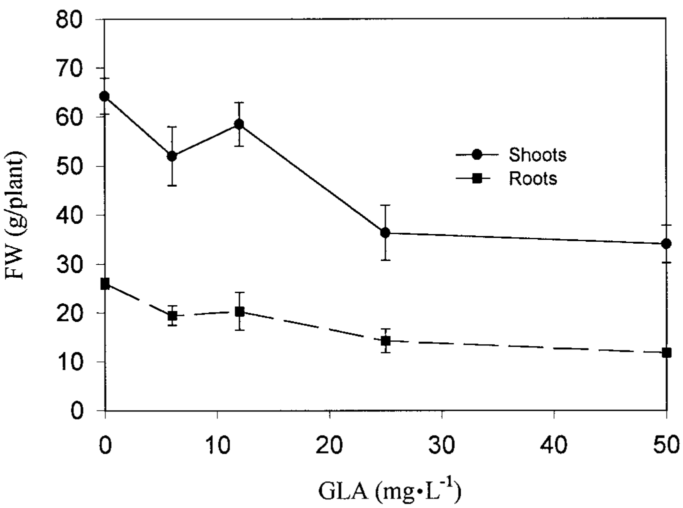

Fig. 1. Fresh weights (FWs) of tomato plants at 6 d after treatment as a function of concentration of GLA in solution. Each symbol represents mean (n = 3) ± 1 SD. Some SD bars are smaller than the data points. See text for trend analysis. Mean FWs of plants with NH_4^+ without GLA are 59 g/plant for shoots and 19 g/plant for roots.

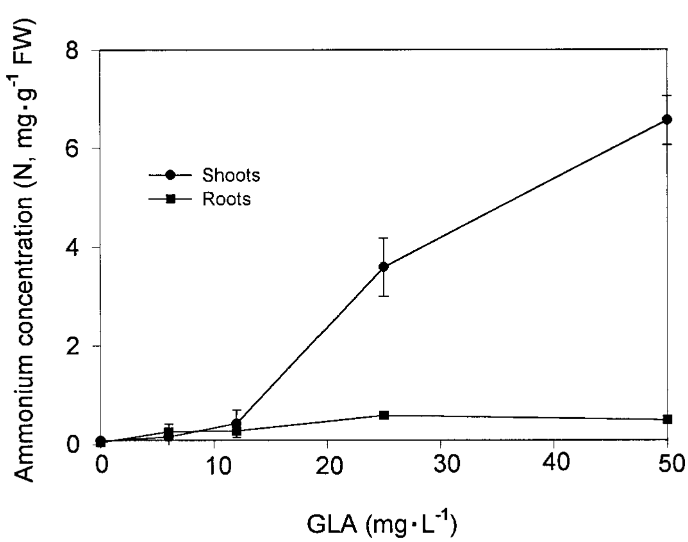

Fig. 2. Ammonium concentrations in tomato plants at 6 d after treatment as a function of concentration of GLA in solution. Each symbol represents mean (n = 3) ± 1 SD. Some SD bars are smaller than the data points. See text for trend analysis. Mean NH_4-N concentrations in plants with NH_4^+ without GLA are 0.35 mg·g^{-1} for shoots and 0.47 mg·g^{-1} for roots.

NH_4^+ analysis (both experiments). Tissue sampling included taking tips of tomato shoots including the first fully expanded leaf on each harvest date and, separately, the entire roots. About 10 g of fresh tissues were homogenized with 25 mL of mixed solution of 1 M KCl and 0.02 M $CuSO_4$ in a blender for 5 min. After vacuum filtration of the homogenized tissue, steam distillation was employed to determine NH_4^+ concentrations in the filtrate (Feng and Barker, 1992).

Results

Dose experiment. At 6 d after treatment (DAT), NH_4^+ toxicity symptoms (Maynard and Barker, 1969) of leaf chlorosis, necrosis, wilting, and cupping appeared on tomato plants treated with GLA at 25 mg·L^{-1}. Plants treated with GLA at 50 mg·L^{-1} were desiccated or totally necrotic. No visible disorders were evident on plants receiving exogenous NH_4^+ or on plants receiving GLA at 6 or 12 mg·L^{-1}. However, tomato shoot fresh weight was inhibited (quadratic trend; $P \leq 0.05$; $y = 64.2 - 1.31x + 0.014x^2$; $R^2 = 0.86$) as GLA concentration increased with NO_3^- nutrition (Fig. 1). Growth inhibition was ≈40% with GLA at 25 or 50 mg·L^{-1} relative to the 0-level of GLA. The fresh weight of tomato shoots grown on NH_4^+ nutrition averaged 59 g/plant and was not significantly different ($P > 0.05$) from that of plants grown with NO_3^- nutrition (63 g/plant) without GLA for 6 d.

Herbicide in solution imparted visible changes on tomato roots, causing them to become progressively thin, sticky, and brown as GLA concentration increased above 6 mg·L^{-1}. Growth suppression increased (linear trend; $P \leq 0.05$; $y = 23.1 - 0.26x$; $r^2 = 0.83$) with increasing herbicide concentrations in solution (Fig. 1). High herbicide levels (25 or 50 mg GLA/L) caused root stunting by 40% to 50% of fresh weight relative to plants receiving no herbicide and NO_3^- nutrition. Exogenously supplied NH_4^+ did not affect ($P > 0.05$) tomato root fresh weight (19 g/plant) relative to that of plants with NO_3^- nutrition without GLA (26 g/plant).

All GLA treatments led to only minor accumulation of NH_4^+ in roots, with no differences ($P > 0.05$) occurring among treatments for which the average NH_4^+ concentration was ≈0.3 mg N/g fresh weight (Fig. 2). However, shoot NH_4^+ levels increased (cubic trend; $P \leq 0.05$; $y = 0.38 - 0.115x + 0.015x^2 - 0.0002x^3$; $R^2 = 0.99$) as herbicide level increased, rising from 0.07 to over 6.5 mg N/g fresh weight (Fig. 2), with a simultaneous increase of the severity of visible symptoms (chlorosis, necrosis, and wilting). Ammonium as a sole N source led to NH_4^+ accumulation in shoots at 0.35 mg N/g and in roots at 0.47 mg N/g. The NH_4^+ concentration from the external supply was significantly ($P \leq 0.05$) higher in roots than in shoots, whereas NH_4^+ accumulation induced by GLA was significantly ($P \leq 0.05$) higher in shoots than in roots (Fig. 2).

Ethylene evolution rose with increases in GLA concentration to 25 mg·L^{-1} (Fig. 3). The GLA treatment at 25 mg·L^{-1} caused the highest ethylene evolution at 6 DAT. The GLA treatment at 50

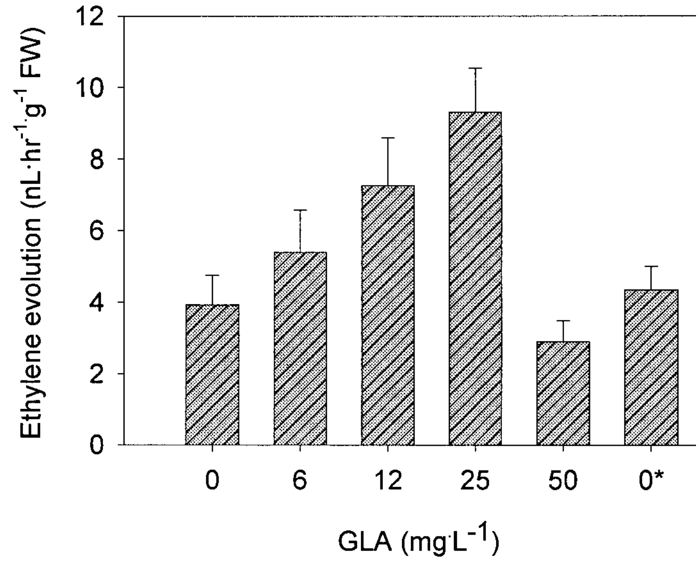

Fig. 3. Ethylene evolution of tomato plants at 6 d after treatment with various concentrations of concentration of GLA in solution or with NH_4^+ without GLA. The 0* designates treatment of NH_4^+ without GLA. Vertical lines above bars represent 1 SD (n = 3).

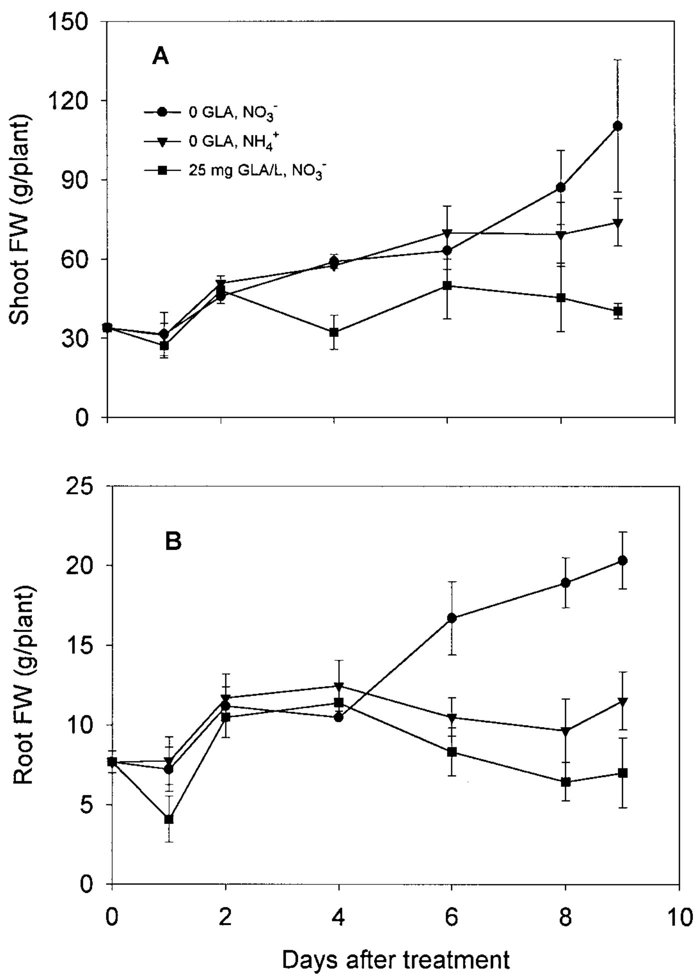

Fig. 4. Time course of tomato (**A**) shoot and (**B**) root fresh weights of plants after GLA treatment at 25 mg·L^{-1} with NO_3^- nutrition or with no GLA application with NO_3^- or NH_4^+ nutrition. In each section, each symbol represents mean (n = 3) ± 1 SD. Some SD bars are smaller than the data points. See text for trend analysis.

mg·L^{-1} desiccated the foliage and depressed ethylene evolution relative to that of the other treatments at 6 DAT. Exogenous NH_4^+ did not cause an increase in ethylene evolution during this time period relative to the treatment with NO_3^- and no GLA.

Time-course of herbicide effect. Tomato plants treated with GLA at 25 mg·L^{-1} developed toxicity symptoms of leaf yellowing and wilting at 6 DAT and were fully necrotic at 9 DAT. Inhibition of tomato shoot growth (Fig. 4A) by GLA occurred at 4 DAT, and inhibition of root growth (Fig. 4B) occurred at 6 DAT. The exogenous NH_4^+ supply did not damage plant appearance at any time and did not suppress growth in the early course of the experiment. However, at the end of the experiment (9 DAT), shoot fresh weight with NH_4^+ nutrition (74 g/plant) was lower than with NO_3^- nutrition without herbicide (110 g/plant) (Fig. 4A). A suppression in root growth by NH_4^+ nutrition, relative to NO_3^- nutrition, was evident at and following 6 DAT (Fig. 4B).

Either GLA application or exogenous NH_4^+ led to NH_4^+ accumulation in plant shoots or roots with time (Fig. 5A). However, the accumulation patterns were different. Nutritional NH_4^+ caused much smaller increases of NH_4^+ accumulation in shoots and roots with time than the GLA treatment. In contrast with the effects from NH_4^+ nutrition, NH_4^+ accumulation induced by GLA was partitioned to shoots and increased with time (Fig. 5A). At 9 DAT, more than 90% of accumulated NH_4^+ in response to GLA was in shoots based on concentrations detected. In shoots, NH_4^+ accumulation caused by GLA was curvilinear (quadratic trend; $P \leq 0.05$; $y = -0.52 + 2.30x - 0.09x^2$; $R^2 = 0.99$) and was up to six times that caused by exogenous NH_4^+, which showed no change ($P > 0.05$) with time (Fig. 5A). In roots, however, exogenously supplied NH_4^+ led to 2 to 3 times higher NH_4^+ accumulation than GLA treatments, although the concentrations were much smaller than those occurring in shoots with GLA treatment (Fig. 5B). The increases in roots were curvilinear with time (with NH_4^+, $y = 0.03 + 0.21x - 0.018x^2$, $R^2 = 0.96$; and with GLA, $y = 0.03 + 0.057x - 0.005x^2$, $R^2 = 0.67$). Nitrate nutrition without GLA had no effect on NH_4^+ accumulation with time.

At 4 DAT, ethylene production by GLA-treated plants exhibited a sharp rise to 8.3 nL·g^{-1}·h^{-1} from the initial rate of 2.6 units (Fig. 6). In a curvilinear trend (cubic regression; $P \leq 0.05$; $y = 2.80 - 0.27x + 0.62x^2 - 0.66x^3$; $R^2 = 0.89$), this increase occurred concurrently with the visual appearance of NH_4^+ toxicity symptoms. When GLA-treated plants died at 9 DAT, their ethylene evolution decreased to the level of plants not treated with herbicide. During the 9-d experimental period, ethylene evolution by tomato plants receiving no herbicide remained low, regardless of the N source, and showed no significant trends with time (Fig. 6).

Discussion

This study demonstrated herbicidal action of root-applied GLA. The increase in shoot NH_4^+ level following root application of GLA was evidence of herbicidal action, since NH_4^+ accumulation is an indicator of glutamine synthetase inhibition (Manderscheid and Wild, 1986; Mersey et al., 1990). In this study, GLA at 25 or 50 mg·L^{-1} in solution caused substantial NH_4^+ accumulation (much greater than 1 mg NH_4^+-N/g fresh weight) in shoot tissue, plant growth suppression, and, within 6 to 9 d, plant death. The increase in shoot NH_4^+ appeared before the onset of symptoms and death. Mersey et al. (1990) and other researchers (Diaz et al., 1995; Lacuesta et al., 1989; Seelye et al., 1995) observed a similar sequence of plant responses with GLA applied

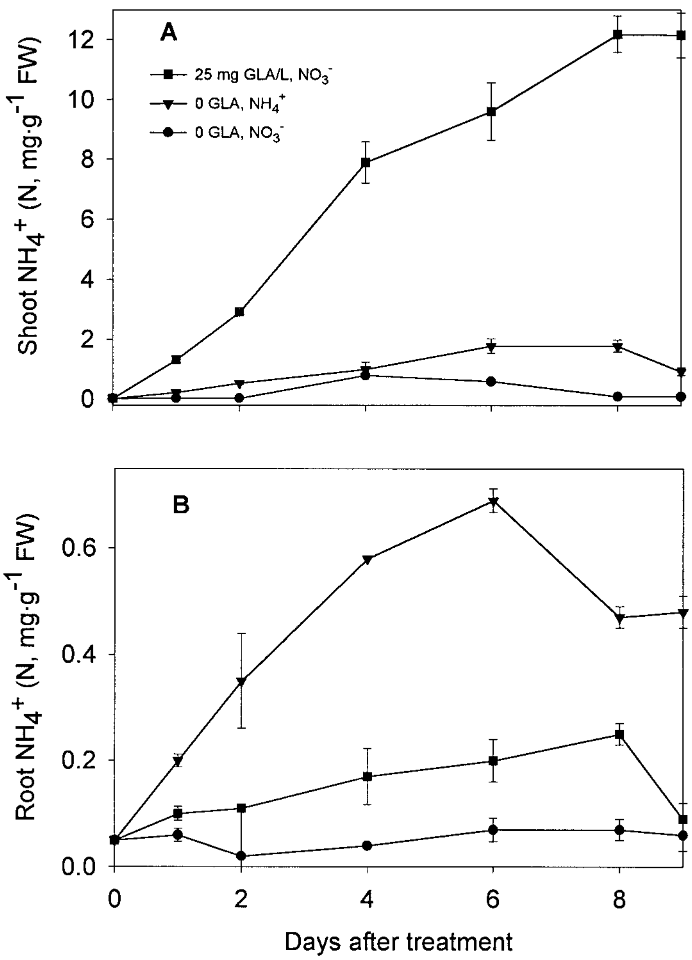

Fig. 5. Time course of NH_4^+ accumulation in tomato (**A**) shoots and (**B**) roots after treatment with GLA at 25 $mg \cdot L^{-1}$ with NO_3^- nutrition or with no GLA application with NO_3^- or NH_4^+ nutrition. In each section, each symbol represents mean (n = 3) ± 1 SD. Some SD bars are smaller than the data points. See text for trend analysis.

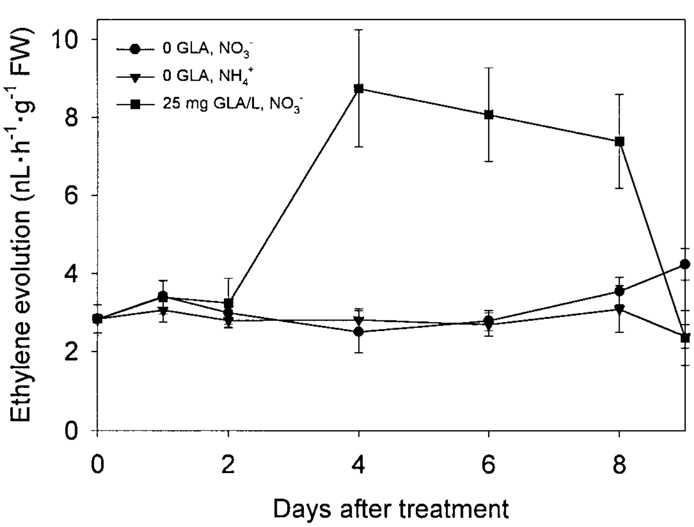

Fig. 6. Time course of ethylene evolution of tomato plants after treatment with GLA at 25 $mg \cdot L^{-1}$ with nitrate nutrition or with no GLA application with NO_3^- or NH_4^+ nutrition. Each symbol represents mean (n = 3) ± 1 SD. Some SD bars are smaller than the data points. See text for trend analysis.

as a foliar spray. In the current study, NH_4^+ concentrations in roots were low and did not relate to appearance of foliar symptoms, even though GLA was applied to the roots. Shoot accumulation exceeding 1 mg NH_4^+-N/g fresh weight following GLA application was sufficient to impart NH_4^+ phytotoxicity (Maynard and Barker, 1969).

Patterns of NH_4^+ accumulation, ethylene evolution, and symptoms of phytotoxicity suggest root absorption and translocation of GLA from roots to shoots. The fact that sharp increases of NH_4^+ occurred in plant shoots and not in roots was taken as evidence of absorption and translocation of GLA. The action site of GLA is the chloroplasts of leaves (Ridely and McNally, 1985), the principal site of reduction of NO_2^- to NH_4^+ in plants and the major site of assimilation of metabolically generated NH_4^+. In the time period of this experiment, no evidence was obtained for production and translocation of NH_4^+ from roots to shoots and subsequent phytotoxicity of NH_4^+. In fact, root NH_4^+ concentration with NH_4^+ in the nutrient solution was higher than that in the shoots, suggesting that the roots were retaining NH_4^+. Following GLA application in solution, leaf NH_4^+ concentrations were 10 to 20 times those in roots depending on the period of exposure to GLA. Furthermore, the relationships among ethylene evolution by shoots, visible symptoms, and the distinct pattern of NH_4^+ accumulation following GLA application to roots also suggested translocation of GLA from roots to shoots and herbicidal action in the shoots.

Ethylene evolution was enhanced following root application of GLA. At 1 d before the appearance of toxicity symptoms, ethylene evolution increased to double or triple the initial rate. Hall et al. (1985) with 2,4-D (2,4-dichlorophenoxyacetic acid) and Harber and Fuchigami (1989) with clopyralid (3,6-dichloro-2-pyridinecarboxylic acid) and picloram (4-amino-3,5,6-trichloro-2-pyridinecarboxylic acid) also demonstrated ethylene evolution by herbicide-treated plants. Ethylene acts as a general signal of various environmental and biological stresses in plants (Abeles et al., 1992) and occurs specifically with plants under stress of NH_4^+ toxicity (Feng and Barker, 1992).

Although the sensitivity to GLA varies with plant species, growth status, and soil and environmental conditions, the effective rate for foliar application is several hundred milligrams of active ingredient per liter (Carlson and Burnside, 1984). That amount is several-fold the maximum root applications shown to be effective herein. This comparison in concentrations does not mean that root applications of GLA are more effective than foliar applications, since the duration of exposure of plants to GLA in nutrient solutions likely exceeds that from a single application of foliar spray. It is clear, however, that root-applied GLA is physiologically active and capable of imparting plant responses similar to those of foliarly applied GLA. These results suggest that GLA present in a soil solution at 25 $mg \cdot L^{-1}$ or higher may result in severe phytotoxicity to tomato. Effects of sublethal concentrations of GLA on field-grown crops require further investigations.

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