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Influence of Nitrogen Form on Exudation Rate, and Ammonium, Amide, and Cation Composition of Xylem Exudate in Tomato[1]

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Abstract. **A shift from NO_3 to NH_4-N nutrition for tomato (*Lycopersicon esculentum* Mill.) plants resulted in a significant decrease in xylem exudation rate within 15 minutes. Ammonium treatment also decreased Ca and Mg concentration in exudate in the 1.5 to 2.5 hour interval after the shift, whereas free NH_4 and amides increased in the same period. Potassium ion concentration did not change in the time interval from 15 minutes to 7 days following the change of N form. Reduced exudate concentration or reduced exudation rate resulted in large decreases in the total amount of K, Ca, and Mg delivered in the presence of NH_4 relative to that of NO_3, and offers a possible explanation for the observed deficiencies of these cations in shoot tissues of plants under conditions of NH_4 toxicity.**

Ammonium fertilization of corn and tomato results in reduced Ca and Mg composition of the whole plant (4, 5, 8, 9, 12), but especially of tissues formed during treatment (3, 10, 17). It has been suggested that NH_4 interferes with H_2O uptake and root exudation in tomato (8, 13, 15). The aim of the present study was to determine whether reduced cation composition of the shoot is the result of decreased flow of xylem contents, reduced cation concn in the xylem sap, or a combinationn of these 2 factors. When tomato is supplied N as NO_3, NO_3 reduction occurs predominantly in the shoot (6). Therefore, it was also of interest to determine the effect of N form on the levels of NH_4 and amides in the exudate, as well as the time dependence of the response to change of N form in the nutrient medium.

Materials and Methods

Seeds of 'Campbell 1327' tomato were germinated in vermiculite. Ten days after emergence, uniform seedlings were transplanted to 4 liter plastic containers filled with quartz sand. The plants were then cultured in a greenhouse for 21 days with modified Hoagland's no. 1 solution (pH 6.3) of the following composition in mM: KH_2PO_4, 1; K_2SO_4, 1; Ca $(NO_3)_2$, 4; $MgSO_4$, 2; $FePO_4$, 6.5×10^{-2}; Sequestrene 330 Fe(Fe_2O_3), 1.1×10^{-2}; H_3BO_3, 4.6×10^{-2}; $MnCl_2 \cdot 4H_2O$, 9.2×10^{-3}; $ZnSO_4 \cdot 7H_2O$, 7.65×10^{-4}; $CuSO_4 \cdot 5H_2O$, 3.21×10^{-4}; $H_2MoO_4 \cdot H_2O$, 1.11×10^{-4}. This nutrient medium provided NO_3 as the sole source of N. Containers were flushed once daily with excess fresh nutrient solution to maintain pH and nutrients at a reasonably constant level.

Experiments were performed under ambient greenhouse conditions, although natural photoperiods were adjusted to 16 hr with supplemental fluorescent lights having an irradiance of 2152 lux. This investigation was conducted during both the summer, when ambient greenhouse temp occasionally exceeded 35°C, as well as during the winter, when it was maintained at 25°. This seasonal temp difference accounted for exudation rate differences between experiments. Experimental treatments were randomized on the greenhouse bench and each treatment was replicated twice, except for the short-term kinetics study, in which samples from 4 replicates were pooled. Treatments were initiated by rapidly flushing each container with excess nutrient solution modified in the following manner: $Ca(NO_3)_2$ was omitted while 4 mM $(NH_4)_2SO_4$ and 4 mM $CaCl_2$ were added. pH was adjusted to 6.3 with NaOH. This medium provided NH_4 as the sole source of N. Plants were detopped at various times after beginning treatment at the same time each day (1330 hr). Detopping was accomplished by making a smooth horizontal cut with a razor blade just above the cotyledonary node. Xylem exudate delivered to the cut stem surface by root pressure was collected with a disposable pipette, transferred to a graduated conical centrifuge tube held over ice, and then frozen until analyzed. Data collected included measurements of exudate volume, determinations of exudate free NH_4 and amides according to a microdistillation procedure (1, 2, 14), and direct measurements of exudate K, Ca, and Mg with a Unicam flame spectrophotometer.

Shoots of detopped plants were dried for 3 days in a forced-air oven at 70°C, weighed, and ground in a Wiley mill to pass a 20 mesh screen. The ground material was ashed in a H_2SO_4-H_2O_2 digest and analyzed for K, Ca, and Mg. Total N was determined by nesslerization and P by an NH_4 molybdate procedure (7). NO_3 content was determined with a NO_3 electrode in aqueous extracts of the dried and ground plant material.

Results

Treatment with NH_4 reduced dry wt gain of shoots of 'Campbell 1327' tomato relative to the NO_3 treatment over a 7 day period (Table 1). The P content of shoot tissue was increased, whereas K, Ca, and Mg were decreased. The total N content per g dry wt of shoot was not affected significantly by N form, although the smaller NH_4-treated plants contained much less NO_3-N than did NO_3-treated plants at 7 days.

Determination of NH_4 in the exudate of plants cultured for 21 days on NO_3 indicated the presence of free NH_4, suggesting that some NO_3 reduction occurred in the roots (Fig. 1).

Table 1. Growth and composition of 'Campbell 1327' tomato shoot tissue as influenced by N form. All plants were maintained on NO_3 as the sole source of N for 21 days, then shifted to NH_4 for up to 7 additional days, or maintained on NO_3.

Treatment (N form)	Time of treatment (days)	Dry wt (g)	NO_3 (µg/g)	Tissue composition (% dry wt)				
				N	P	K	Ca	Mg
NO_3	3	4.724	6929	5.89	.90	5.89	3.29	.83
	5	6.114	6800	5.70	.95	5.80	3.50	.84
	7	8.786	7000	5.30	.96	6.00	3.40	.69
NH_4	3	4.152	4575	6.18	1.13	6.01	2.79	.60
	5	5.355	3000	5.60	1.27	5.15	2.40	.47
	7	6.740	1700	5.60	1.30	5.05	2.40	.42
LSD, 5%		.927	1200	NS	.09	.46	.31	.06

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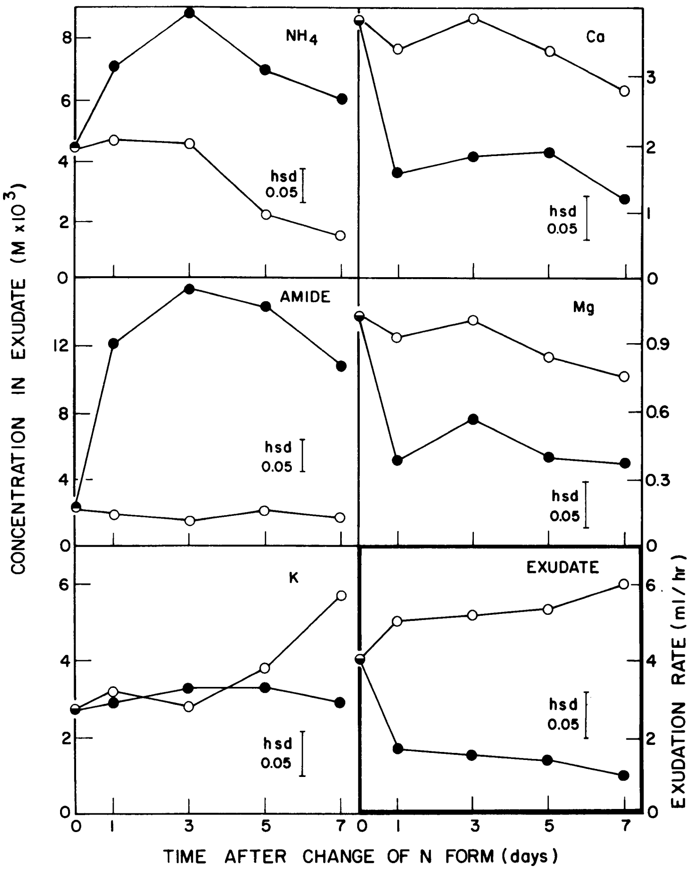

Fig. 1. The effect of N form on the concn of NH_4, amides, K, Ca, and Mg in the xylem exudate of detopped 'Campbell 1327' tomato plants, as well as on exudation rate. After 21 days pretreatment with NO_3, plants were switched to NH_4-N at zero time or retained on NO_3-N and detopped at the times indicated after the shift. Open symbols represent measurements from plants treated with NO_3, closed symbols those from NH_4 treatments.

During the 7 day experimental period, the NH_4 concn of exudate from the NO_3 treatment decreased, possibly reflecting greater utilization of N in the roots with continued growth. Upon shifting from NO_3 to NH_4, however, elevated NH_4 concn was detected by day 1 and amounted to 4 times that of the NO_3 treatment by day 7. The amide concn in exudate experienced a sharp increase in response to the NO_3 to NH_4 shift, whereas that of the NO_3 treatment remained unchanged over the 7 day treatment period. Inorganic cation concn in exudate responded to NH_4 in a different direction than did NH_4 and amides, or not at all. Potassium concn, for example, remained unchanged by a shift to NH_4. On the other hand, both Ca and Mg concn in exudate declined significantly 1 day after the shift, and were maintained at these lower levels until day 7. Another consequence of the NO_3 to NH_4 shift was a significant reduction in exudation rate. One day after the shift, NH_4 had abruptly diminished the capability for exudation, following which the rate continued to decline more slowly. At the same time, the exudation rate of plants maintained on NO_3 increased gradually.

If exudation rate as well as concn of constituents in exudate are considered, a more comprehensive view of the toal amount (dosage) of a constituent in exudate is obtained (Fig. 2). For example, even though the concn of free NH_4 in the exudate of the NH_4 treatment rose to 400% that of the NO_3 treatment by day 7 (Fig. 1), the total amount of NH_4 delivered was only 66% that of the NO_3 treatment (Fig. 2), due primarily to the much lower exudation rates of the NH_4 treatments (Fig. 1) counteracting the increased concn. On the other hand, the amount of amides delivered in exudate increased significantly in response to NH_4 during the early part of the treatment, but declined to the same level as found in the NO_3 treatment by day 7 (Fig. 2), again due to the slower exudation rate. Potassium, Ca, and Mg dosage declined significantly after only 1 day of exposure to NH_4, and constituted only 7 to 9% of the NO_3 treatment rate by day 7 (Fig. 2).

Since the greatest changes in exudation rate and concn of exudate constituents had already occurred by day 1 of the treatment period (Fig. 1), it was of further interest to determine how rapidly these effects occur following a N form shift. Therefore, exudates were collected from plants detopped at hourly intervals up to 4.5 to 5.5 hr after a NO_3 to NH_4 shift, or conversely, after an NH_4 to NO_3 shift following a 3 day NH_4 pretreatment (Fig. 3). The NO_3 to NH_4 shift triggered a rise in free NH_4 concn after only 1.5 hr. The reciprocal NH_4 to NO_3 shift had the opposite effect. Amides in the exudate experienced even larger concn changes in response to N form shifts. The reciprocal NH_4 to NO_3 shift resulted in a decline of amide concn similar to that of the NH_4 ions. The NO_3 to NH_4 transition induced no change in the K concn of exudate during the treatment period up to 5.5 hr. However, the reciprocal NH_4 to NO_3 transition resulted in a sharp increase in K concn. Ammonium treatment also caused an early decrease of Ca concn, followed by a partial recovery. The reciprocal shift resulted in a more gradual increase in Ca concn. This recovery, however, represented only 71% of the zero time NO_3 treatment level of Ca, indicating that recovery was still incomplete within the time frame of the test period (up to 5.5 hr). The Mg response pattern paralleled that of Ca in the NO_3 to NH_4 transition. In contrast to Ca, however, the reciprocal NH_4 to NO_3

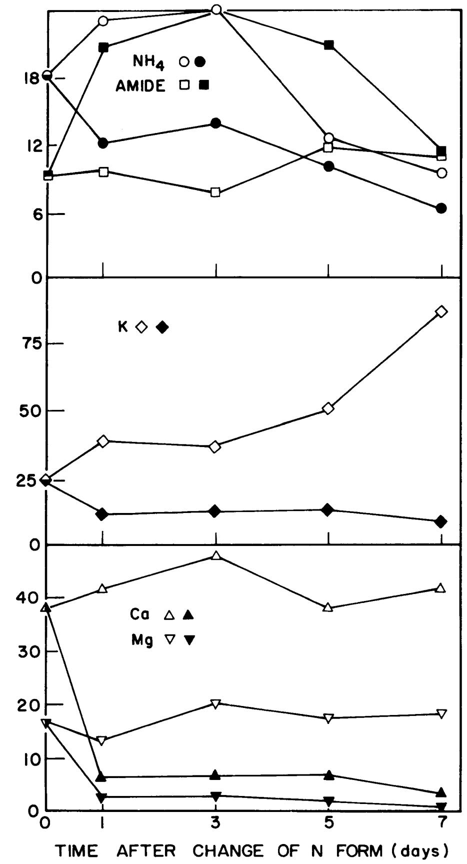

Fig. 2. The effect of N form on the total amount of free NH_4, amides, K, Ca, and Mg delivered in the xylem exudate of detopped tomato plants. The data were calculated from the exudate concn of each constituent and exudation rate presented in Fig. 1. Symbols are the same as in Fig. 1.

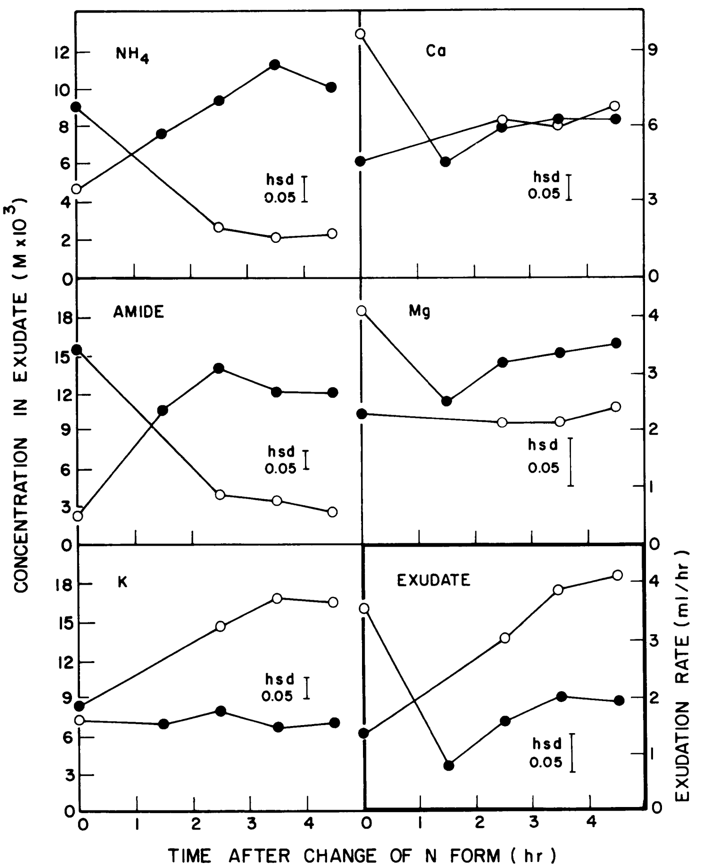

Fig. 3. The effect of N form on the concn of NH_4, amides, K, Ca, and Mg in the xylem exudate of detopped tomato plants, as well as on exudation rate. After 24 days pretreatment with NO_3-N, one group of plants was shifted to NH_4-N at zero time and detopped at the times indicated after the switch. Another group was pretreated with NO_3 for 21 days, switched to NH_4 for 3 days, and switched back to NO_3 at zero time. Symbols are the same as in Fig. 1.

transition resulted in no significant recovery of Mg concn during the test period. A shift to NH_4 induced the greatest drop in exudation rate early in the treatment period, once again indicating that the change in exudation occurred more rapidly than the shortest time interval measured (1.5 hr). The initial decline was followed by a partial temporary recovery in the continued presence of NH_4 (Fig. 3). This recovery lasted no more than 24 hr before entering a slower, irreversible decline (Fig. 1). Plants having received the 3-day NH_4 pretreatment exhibited an exudation rate only 38% that of the NO_3 treatment. Following the reciprocal NH_4 to NO_3 shift, however, the exudation rate recovered rapidly and reached 117% of the NO_3 treatment by 4.5 to 5.5 hr.

The NH_4 dosage in exudate increased, after an initial sharp decline, to only 120% of the zero time NO_3 treatment by 5.5 hr after the NO_3 to NH_4 transition (Fig. 4). Thus, a significant increase in NH_4 concn was compensated for by an almost equally significant decrease in exudation rate. Although the reciprocal NH_4 to NO_3 shift was accompanied by a substantial drop in NH_4 concn (Fig. 3), this drop was compensated for by a recovery of exudation rate, with the result that the total amount of NH_4 delivered declined to only 78% of the zero time NO_3 control at the end of the treatment period (Fig. 4). The dosage responses to a NO_3 to NH_4 shift were qualitatively similar for all 3 cations determined, but proportionally greater for the divalent cations. The decline in total amount of K delivered in xylem exudate was exclusively due to the decline in exudation rate (Fig. 3). The reduced amounts of Ca and Mg delivered were due to a combination of both decreased exudation rate and decreased concn. All cations subsequently experienced a partial recovery in delivery following the initial decline. The reciprocal NH_4 to NO_3 shift resulted in recovery in dosage of all 3 cations. The large change in K concn is attributable to a considerable increase in both exudation rate and exudate concn following the reciprocal shift; this is the only treatment studied which affected K concn in exudate. Calcium and Mg experienced a more modest degree of recovery of amount delivered, due principally to increasing exudation rate throughout the test period.

In view of the rapid responses of exudation rate and divalent cation concn to NH_4 treatment, it was decided to test the exudation response over even shorter time periods (Fig. 5). The effect of shifting intact plants from NO_3 to NH_4 and detopping caused an immediate (zero to 15 min) decline in exudation rate to 40% of the initial rate. This was followed by a further decline for about 30 min and then by a gradual partial recovery. No significant changes in K, Ca, or Mg concn in exudate were detected in response to the NO_3 to NH_4 shift during the 90 min time course. However, collection of exudate from the same detopped plant at successive 15 min intervals indicated a gradual irreversible decline in the ability of the root to deliver exudate to the cut surface by either NO_3 or NH_4 treatments. Unlike the situation in which exudate was collected for only a single 15 min interval following detopping, the concn of cations in exudate collected at successive 15 min intervals from the same cut stump increased, with NO_3 treatments generally increasing most. A comparison of the short-time responses to NH_4 suggest that effects on exudation rate

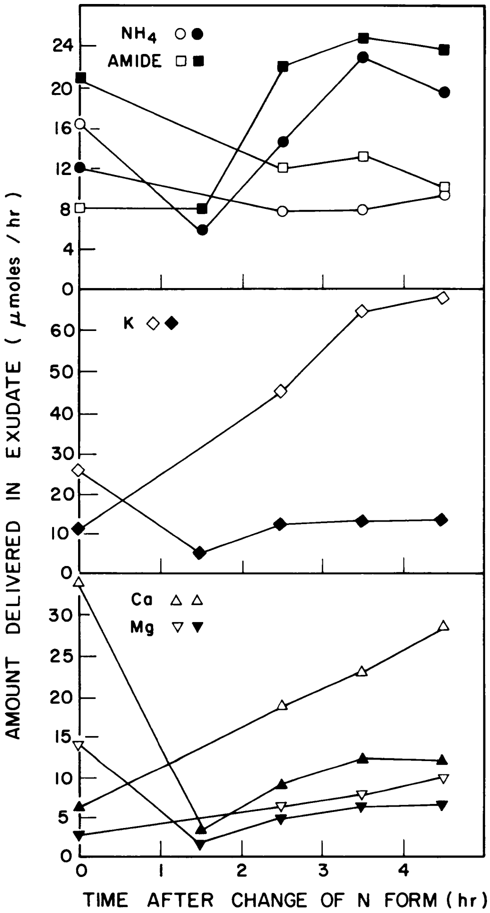

Fig. 4. The effect of N form on the total amount of free NH_4, amides, K, Ca, and Mg delivered in the xylem exudate of detopped tomato plants. Open symbols represent measurements from plants treated with NO_3, closed symbols those from NH_4 treatments.

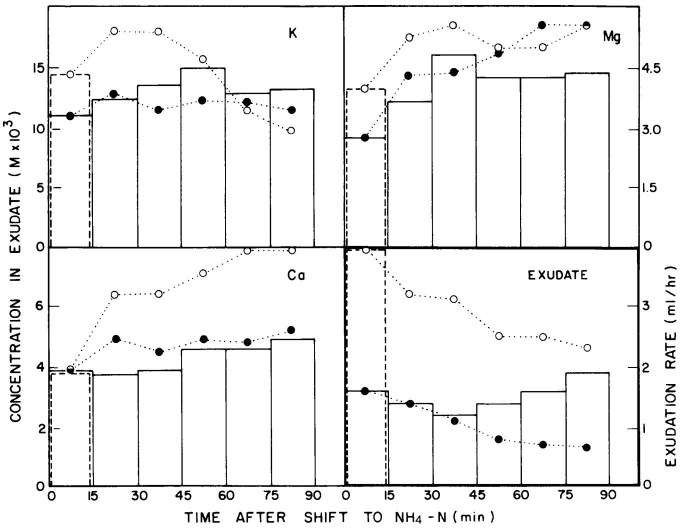

Fig. 5. Short-term responses of exudation rate and exudate concn of K, Ca, and Mg to a NO_3 to NH_4 shift at zero time. Bar graphs represent measurements from plants detopped at the beginning of each 15 min interval indicated. Dashed bars and open symbols represent measurements from detopped NO_3 treatments, solid bars and closed symbols NH_4 treatments. Dotted lines represent measurements from successive collections of exudate from the same detopped plants.

occur earlier than effects on cation concn. Exudation responses to a NO_3 to NH_4 transition are of the order of min (perhaps sec), whereas divalent cations respond only after hours.

Discussion

Quality as well as quantity of N nutrition has a pronounced effect on the growth and productivity of most economically important crop plants. In the case of tomato, the presence of NH_4 reduces dry wt gain (Table 1) as well as shoot and root growth, in comparison with NO_3 treatments. Although the results of the present study indicated no significant differences between the N composition of shoots of NO_3 and NH_4 treatments if expressed on a dry wt basis, this can be misleading unless NH_4-induced growth reduction is also accounted for. Phosphorous composition increased progressively with time of NH_4 treatment, probably because Pi served as a counterion for the NH_4 cation. Cation composition of shoots, however, decreased progressively with time of exposure to NH_4, with the most pronounced effects involving the divalent cations. All of these effects are consistent with observed symptoms of the NH_4 toxicity syndrome in tomato (17).

The observed changes in shoot composition resulting from NH_4 treatment presumably arise from qualitative and quantitative changes in root uptake and subsequent delivery of these constituents to the shoot. Xylem exudation by detopped plants is assumed to reflect the qualitative composition of the transpiration stream in intact plants. However, one inherent weakness of extrapolating performance of detopped to intact plants includes the additional stress of loss of a continued supply of carbohydrate needed to maintain root pressure. Another is that, without a shoot, exudation rate cannot reflect transpiration rate. Nevertheless, exudation responses are useful as measures of root resistance to H_2O and solutes. Exudation responses from the present investigation suggest that NH_4 interferes with the root uptake of divalent cations and H_2O. It has not yet been determined whether the observed effect of NH_4 on exudation rate is due to a direct effect on hydraulic conductivity of root membranes or to an indirect effect on the driving force for H_2O uptake. Thus, the water stress symptoms of leaf curl and wilting associated with NH_4 toxicity (17) are likely due to increased root resistance to H_2O movement.

The time dependence and directions of change in concn of exudate constituents varied widely in response to a NO_3 to NH_4 shift. Free NH_4 and amides, for instance, responded by significant increases in exudate concn in the 1.5 to 2.5 hr interval following the shift. Although the absolute increase in amides was much greater than that of NH_4, detoxification mechanisms such as glutamine synthetase and glutamic dehydrogenase failed to retard a slow but steady rise in exudate concn of free NH_4 for 3 days following the shift (Fig. 1). When NH_4 toxicity symptoms first began to appear (4 to 5 days after starting treatment), both concn (Fig. 1) as well as total amount (Fig. 2) of amides and NH_4 in exudate increased concurrently with progressive development of toxicity symptoms relative to NH_4 in the NO_3 treatment (Fig. 1). At the same time, the capacity to detoxify NH_4 by amidation declined (Fig. 1 and 2). Exhaustion of carbohydrate reserves could account for both observations. The reciprocal NH_4 to NO_3 shift following a 3-day NH_4 pretreatment resulted in complete reversal of amide concn back to the zero time NO_3 treatment level, while free NH_4 concn actually fell below the NO_3 treatment level (Fig. 3).

An induced K deficiency in tomato shoot tissue is considered an important characteristic of NH_4 toxicity in tomato (11). In the present investigation, the 7 day exposure to NH_4 reduced K composition of the shoot to 84% of the NO_3-treated plants (Table 1). Although the exudate K concn remained unchanged over the NH_4-treatment period (Fig. 1), the total amount of K delivered by day 7 declined to 35% of the zero time level, or 9% of the NO_3-treated plants of the same age. Thus, reduced exudation rate alone (and by inference reduced H_2O movement in the intact plant) may account for NH_4-induced K deficiency. Although the NO_3 to NH_4 shift did not affect the concn of K in exudate, the reciprocal shift did cause increases in K concn (Fig. 3) and in total K delivered (Fig. 4).

Among the most significant ramifications of NH_4 toxicity is an induced deficiency of Ca and Mg, which has implications for blossom end rot in tomatoes (17) and grass tetany in foraging cattle (16). Although neither divalent cation decreased significantly in concn during the first 90 min following a NO_3 to NH_4 shift (Fig. 5), both decreased substantially in the 90 to 150 min interval (Fig. 3). Thus, a lag period of at least 90 min occurred before decreased Ca and Mg concn were detected. Both cations also experienced a partial recovery in concn, which may represent compensation for NH_4 by switching on of detoxification mechanisms, but by 24 hr or less, concn of Ca and Mg once again began a substantial and irreversible decline (Fig. 1). The reciprocal shift resulted in a slow, partial recovery of Ca but not of Mg (Fig. 3). Recovery of depleted pools of the divalent cations within the root quite possibly accounts for the delay in reappearance of Ca and Mg in the xylem exudate.

Of all the NH_4 response parameters measured, changes in exudation rate were the most rapid and had the greatest impact on amount of constituents delivered in the exudate. The shortest response time measurable in the present study was 15 min, during which a NO_3 to NH_4 shift reduced the exudation rate to 40% that of NO_3-treated plants detopped at the same time (Fig. 5). Visual observation, however, indicated that the exudation response to NH_4 actually occurred within a few sec. It was also noteworthy that tomato roots underwent a gradual, irreversible loss of exudate-yielding ability following detopping, irrespective of N form (Fig. 5). Thus, successive collections of exudate from the same detopped plants for up to 1 hr in previous experiments (Fig. 1 and 3) actually represented the pooled result of a progressively declining exudation rate. Periodic recutting of the surface of the stump did not restore exudation. The effect of NH_4 on exudation, then, was to hasten the natural decline in rate following detopping, relative to NO_3 treatments. However, plants detopped during the second 45 min interval following a NO_3 to NH_4 shift partially recovered in exudation rate in the 15 min period immediately after detopping, whereas those detopped during the first 45 min interval decreased in exudation rate. This recovery also probably reflects gradual compensation by an NH_4 detoxification mechanism whose sustained activity required the intactness of the plant.

Another result of successive collections of exudate from the same plant is a significantly increased exudate concn of cations above that found in the first 15 min collection. A likely explanation for this result exists for both NO_3 and NH_4 treatments. In the case of a transition to NH_4, H_2O uptake and movement in the xylem was inhibited almost immediately, whereas a significant drop in divalent cation concn (intact plant function) was not seen before 1.5 hr (Fig. 5). In the case of the NO_3 treatments, cations continued to be taken up by the root, independent of H_2O flux, whereas the effect of detopping was a progressive loss of exudation ability. In either case, the sluggish acropetal movement of H_2O resulted in an accumulation of cations in the xylem sap.

The results of the present investigation suggest that short-time root exudation responses of the order of sec obtained under controlled-environment conditions would be a valuable tool to determine whether the primary action of NH_4 involves an increase in root resistance or a decrease in driving force for H_2O uptake.

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Combining Ability of Three *Lycopersicon* Species for Resistance to *Corynebacterium michiganense*[1]

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Additional index words. heritability, disease resistance, tomato breeding

Abstract. **Estimates of heritability and general and specific combining ability for resistance of tomato to *Corynebacterium michiganense* (E. F. Sm.) H. L. Jens. were made, using a half diallel with 6 parental entries. Both the general and the specific combining abilities of the parents differed. Additive variation accounted for 74% (narrow sense heritability) of the total variation, suggesting that a large part of the observed variation is fixable in true-breeding strains.**

Infection of tomato crops with *Corynebacterium michiganese,* the causal organism of bacterial canker, results in variable losses. Severity of the disease ranges from occasional wilting to death of the plant. Some of the common symptoms, all of which may or may not be present on the infected plants, are: unilateral wilting of leaves, death of growing points, wilting of the plants and formation of stem cankers. Resistance has been reported in the *Lycopersicon pimpinellifolium* and *L. hirsutum* (1, 6, 8). In *L. esculentum,* the cultivar 'Bulgaria 12', from a hybrid with *L. pimpinellifolium,* has been reported to be resistant (3) but it is small fruited and unacceptable in the U.S.

The purpose of this study was to determine the inheritance of bacterial canker resistance to facilitate selection of parents for use in breeding populations and to interpret the results in terms of possible breeding procedures.

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