

Effects of NH₄ and NO₃ Nutrition with and without pH Adjustment on Tomato Growth, Ion Composition, and Water Relations¹

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Abstract. Fertilization of tomato (*Lycopersicon esculentum* Mill.) in solution culture with NH₄-N resulted in reduced shoot and root concentration of Ca, Mg, K, P, and NO₃, increased leaf and root resistances to water flux, and decreased water use efficiency as compared to plants cultured with NO₃-N. Solution adjustment to pH 6.5 decreased shoot/root fresh weight ratio with both N forms; decreased leaf diffusive resistance and water stress but increased root resistance to water flux and shoot NH₄ concentration under NH₄-N nutrition. Solution pH had little effect on tissue ion concentration.

Ammonium-N, as compared to NO₃-N, has resulted in lower plant Ca and Mg concn and higher anion concn, especially phosphate (1, 5, 7, 14, 16, 21), produced leaf and stem lesions (9, 18), reduced growth (1, 17, 18), caused root injury (29), and inhibited water uptake and root exudation and decreased leaf water potential (24).

The detrimental effects of NH₄ nutrition have been related to root environment acidity (11, 22). Maintaining pH near neutrality has resulted in nearly normal growth of plants under NH₄-N (3, 4, 6, 7, 11, 31). The beneficial effects of acidity control have been attributed to increased Ca supply (22), a general increase in cation absorption by roots (11), or to increased conversion of NH₄ to nontoxic metabolites in the root (3, 4).

The influence of N form, with and without pH adjustment on growth, ion concn, and water relations of tomato in solution culture were determined in an attempt to elucidate the relationship between nutrition and water stress.

Materials and Methods

Seeds of Missouri breeding line 76-1-60-8 were sown in vermiculite. Fifty-four uniform seedlings were transferred 18 days later to aerated NO₃-N (12.5 meq/liter) solutions in a controlled environment chamber. Plants were supported by styro-foam stoppers, the roots extending through a central hole into the solution contained in 0.946 liter blackened glass jars. The growth chamber was maintained at 16-hr photoperiod (24°C, ca. 70% RH) and 8-hr nyctoperiod (16°C). Light intensity at plant ht was 1200-1500 ft-c.

Following 3 weeks growth in the 12.5 meq NO₃/liter solution with solution replacement on alternate days, plants were subjected to the following factorially combined treatments: 20.0 meq N/liter as NO₃-N or NH₄-N; pH regimes (no pH adjustment, pH adjustment to 4.0 or 6.5); and length of treatment (1, 2, or 3 weeks). Treatments were arranged in completely randomized design with 3 single-plant replicates. All data except initial solution pH and electrical conductivity (EC) were subjected to analysis of variance.

Solutions were formulated to supply Ca, Mg, K and H₂PO₄ at 15, 4, 6 and 1 meq/liter, respectively, and micronutrients as suggested by Hoagland (12). The only ions varying in concn besides NO₃ and NH₄ were Cl and SO₄. Solutions were prepared in 40-liter volumes and pH's were adjusted with 0.1N NaOH or HCl. Solutions in the jars were replaced on alternate days during the first 2 weeks and daily in the 3rd week.

For each of the 18 plants harvested at the end of a time

period, plant fresh wt and solution use were determined gravimetrically at each solution replacement. The pH and EC of the remaining solution prior to solution replacement were determined. On the last day of each week, water losses from both intact plants and excised tops (cut under water) in 3-hr periods were determined. Shoot and root fresh wt and leaf area (Lambda portable leaf area meter, Model LI-3000) were determined.

Shoots and roots were dried in a forced-air oven at 65°C and ground in a Wiley mill to pass 20-mesh screen. Root samples were composited across time periods to increase sample size. Total Ca and Mg were determined with an atomic absorption spectrophotometer and total K with a flame photometer. Phosphorus was determined with an ammonium molybdate procedure (13). Tissue NO₃ (20) and NH₄ (19) were determined potentiometrically.

Abaxial leaf diffusive resistance (R_L) was determined with a calibrated Lambda diffusive resistance meter and a horizontal diffusion porometer (15). Leaf xylem pressure potential (ψ_p) was determined with a pressure chamber (25). Three midday determinations per plant of both R_L and ψ_p were made at 2-day intervals on each of the 18 plants harvested each week.

Results

Growth. Growth was greater with N supplied as NO₃. Plant fresh wt and leaf area increased with time under NO₃-N but remained constant under NH₄-N nutrition (Table 1). Solution pH was without effect on plant fresh wt or leaf area. Shoot/root fresh wt ratio was reduced by NO₃-N in the first week and increased by NH₄-N in the third week (Table 2). Under each pH regime, the shoot/root ratio was greater under NH₄-N, but the ratio was reduced with both N forms by solution adjustment to pH 6.5 (Table 2).

Tissue composition. Ammonium nutrition decreased the Ca, Mg, K, P, and NO₃ concn of both shoots and roots (Tables 3

Table 1. Fresh wt and leaf area of tomato plants as influenced by solution N form and length of treatment.²

N form	Length of treatment (weeks)	Plant fresh wt (g)	Leaf area (cm ²)
NO ₃	1	204.7c	2173c
	2	291.6b	3259b
	3	393.4a	4451a
NH ₄	1	119.1d	1481d
	2	118.4d	1370d
	3	125.9d	1184d

²Mean separation within a column by Duncan's multiple range test, 5% level.

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Table 2. Tomato shoot/root fresh wt ratio as influenced by solution N form, solution pH, and length of treatment.^Z

N form	Shoot/root fresh wt ratio					
	Weeks of treatment			pH		
	1	2	3	Control	4.0	3.5
NO ₃	3.150c	3.637b	3.705b	3.611b	3.668b	3.213c
NH ₄	3.756b	3.887b	4.647a	4.250a	4.180a	3.860b

^ZMean separation within weeks of treatment or pH by Duncan's multiple range test 5% level.

and 5). In general, shoot concn of these ions decreased with increasing length of treatment. Whereas NH₄-N increased shoot NH₄ concn, it did not affect root NH₄ concn. Root Ca concn of NH₄-plants was very low, being only 2.18% that of roots grown with NO₃-N. Initial solution pH did not affect root ion concn, but changed shoot Mg, P, and NH₄ concn (Table 4). Under NO₃-N, Mg and NH₄ concn were unaffected by solution pH, but shoot P concn was increased in the order pH 6.5 > pH 4.0 > control. Under NH₄-N, shoot P concn was unaffected by solution pH and shoot NH₄ concn was increased by adjustment to pH 6.5. As compared to the control, shoot Mg was increased by solution adjustment to pH 4.0, and adjustment to pH 6.5 gave an intermediate Mg concn.

Abaxial leaf diffusivity resistance (R_L). The R_L was increased by NH₄ nutrition, especially in treatment weeks 2 and 3 (Table 6). While solution pH did not consistently affect R_L of NO₃-plants, under NH₄ nutrition R_L in treatment weeks 2 and 3 were increased in the order control > pH 4.0 > pH 6.5.

Leaf xylem pressure potential (ψ_p). The ψ_p was decreased (more negative) by NH₄ nutrition during treatment weeks 2 and 3 (Table 6). While solution pH did not affect ψ_p of NO₃-plants, under NH₄ nutrition solution adjustment to pH 6.5 increased ψ_p (less negative) in the third week of treatment.

Transpiration rate. Transpiration rates for both intact plants and excised plant tops were reduced by NH₄ nutrition (Table 7). Since the interaction of N form × solution pH × treatment length was not significant, mean values for 3 weeks of treatment are shown. Solution pH under either N form did not influence the transpiration rates of intact plants. With both N forms, however, transpiration rates of excised plant shoots were increased by solution adjustment to pH 6.5. Adjustment of NH₄ solutions to pH 6.5 gave an excised shoot transpiration rate similar to that of shoots under NO₃-N without solution pH adjustment or adjustment to pH 4.0.

The difference in transpiration rates between excised shoots and intact plants was used as an estimate of root resistance to water flux. Whereas under NO₃ nutrition, the transpiration rates of intact plants and excised shoots were the same, the excised shoots of NH₄-plants showed greater transpiration rates than intact NH₄-plants. This increased root resistance under NH₄

Table 3. The Ca, Mg, K, P, NO₃, and NH₄ concn of tomato shoots as influenced by solution N form and length of treatment.^Z

N form	Length of treatment (wks)	Shoot composition—dry wt basis					
		Ca (%)	Mg (%)	K (%)	P (%)	NO ₃ (ppm)	NH ₄ (ppm)
NO ₃	1	3.81a	0.81a	3.66a	0.99a	13306a	292c
	2	3.34b	0.77a	3.11b	0.99ab	12903a	252c
	3	3.05b	0.62c	3.14b	0.97c	13181a	195c
NH ₄	1	3.06b	0.70b	2.64c	0.97c	3600b	940a
	2	2.09c	0.51d	1.93d	0.97c	1667c	495b
	3	1.71d	0.42e	1.91d	0.98bc	1173c	504b

^ZMean separation within columns by Duncan's multiple range test, 5% level.

Table 4. The Mg, P, and NH₄ concn of tomato shoots as influenced by solution N form and solution pH.^Z

N form	pH	Shoot composition—dry wt basis		
		Mg (%)	P (%)	NH ₄ (ppm)
NO ₃	Control	0.71a	0.96c	214c
	4.0	0.73a	0.99b	243c
	6.5	0.76a	1.00a	281c
NH ₄	Control	0.50c	0.96c	541b
	4.0	0.58b	0.98bc	605b
	6.5	0.55bc	0.98bc	792a

^ZMean separation within columns by Duncan's multiple range test, 5% level.

nutrition was particularly pronounced in solutions adjusted to pH 6.5.

Solution uptake. Solution uptake per g plant fresh wt increase per week was greater for NH₄-plants, particularly for those plants grown in solutions adjusted to pH 4.0 (Table 7).

Solution pH and electrical conductivity. The pH of NO₃-N solutions increased to near neutrality irrespective of initial pH regime, while NH₄ nutrition resulted in solution acidification to approx pH 3.5 irrespective of initial pH regime (Table 8). Solution pH and EC values stabilized after 5–6 hr. Solution EC increased with time for both N sources with values for NH₄ solutions being greater than for NO₃ solutions initially and at the time of solution change.

Discussion

Less plant growth from NH₄ nutrition is well documented (1, 17, 18). The NH₄ ion or NH₃ has been reported to accelerate respiratory breakdown of carbohydrates (2), uncouple photosynthetic phosphorylation (10), and result in disruption of chloroplast membranes (23). The increased water stress shown by NH₄-plants (Table 6) would contribute directly to restricted growth. The toxic effect of NH₄-N on growth was further shown by the constancy of plant fresh wt and leaf area with time under NH₄-N as contrasted to their increases under NO₃-N nutrition.

The decrease in tissue Ca and Mg with NH₄ nutrition has also been well documented (1, 5, 7, 14, 16, 21). Tissue K also has been decreased by NH₄ nutrition (7, 32). In contradiction to our observed decrease, tissue P has been reported to be increased by NH₄-N (5, 16, 21). The increase in tissue NO₃ and NH₄ concn by NO₃- and NH₄-nutritions, respectively, has been reported previously (8). The reduction in tissue ion concn with increasing exposure time may be explained by growth dilution under NO₃-N. Loss of membrane integrity, possibly as a result of Ca deficiency (23, 30) under NH₄ nutrition, may explain reduced uptake and/or increased loss of ions.

Previous studies (3, 4, 31) have shown that solution pH adjustment to neutrality increased NH₄ utilization and near normal growth ensued. In this study, solution pH did not affect plant fresh wt or leaf area but initial solution adjustment to pH 6.5 resulted in reduced shoot/root fresh wt ratios of plants

Table 5. The Ca, Mg, K, P, NO₃, and NH₄ concn of tomato roots as influenced by solution N form.^Z

N form	Root composition—dry wt basis					
	Ca (%)	Mg (%)	K (%)	P (%)	NO ₃ (ppm)	NH ₄ (ppm)
NO ₃	2.56a	0.96a	2.14a	1.12a	9674a	135a
NH ₄	0.06b	0.25b	1.11b	0.99b	582b	118a

^ZMean separation within columns by Duncan's multiple range test, 5% level.

Table 6. Abaxial leaf diffusive resistance and leaf xylem pressure potential as influenced by solution N form, solution pH, and length of treatment.^Z

N form		Leaf diffusive resistance (sec cm ⁻¹)			Leaf xylem pressure potential (-bars)		
		Weeks of treatment			Weeks of treatment		
		1	2	3	1	2	3
NO ₃	Control	3.85j	5.36ghi	5.18ghi	3.57i	4.13e	3.69hi
	4.0	3.92j	5.56gh	3.81j	3.33j	3.98efg	4.04ef
	6.5	3.60j	6.32f	3.86j	3.51ij	4.02ef	3.89fg
NH ₄	Control	4.89i	19.49b	20.43a	3.58i	4.65d	6.08a
	4.0	5.65g	16.72c	14.81d	3.59hi	4.97c	5.65b
	6.5	5.04hi	12.11e	11.96e	3.78gh	4.74d	5.04c

^ZMean separation within columns and rows for abaxial leaf diffusive resistance and for leaf xylem pressure potential by Duncan's multiple range test, 5% level.

Table 7. Transpiration rates of intact plants and excised shoots and solution uptake as influenced by solution N form and solution pH.

N form	pH	Transpiration rate (g dm ⁻² 3h ⁻¹) ^{ZY}		Solution uptake per g fresh wt per week ^{ZY}
		Intact plant	Excised top	
NO ₃	Control	2.001a	2.020b	21.77c
	4.0	2.097a	2.011b	19.39c
	6.5	2.277a	2.252a	22.66c
NH ₄	Control	1.173b	1.625c	46.81b
	4.0	1.277b	1.615c	128.71a
	6.5	1.349b	1.910b	55.33b

^ZMean separation by Duncan's multiple range test, 5% level.

^YValues are means for the 3 weeks of treatment.

grown with both N forms (Table 2). Roots of NH₄-plants grown in solutions periodically adjusted to pH 6.5 were not discolored as they were under the other pH regimes. Ammonium nutrition has been shown to cause root injury (26, 29) while maintenance of pH 7.0 has promoted root growth under NH₄ nutrition (26).

The decreased ψ_p with NH₄ nutrition (Table 6) probably resulted from increased root resistance to water flux. Slatyer (27) suggested that water uptake inhibition resulted from a change in membrane structure. Loss of membrane integrity by NH₄-induced Ca deficiency has been related to the toxic effects of NH₄ on chloroplasts (23) and mitochondria (30). The inhibiting effect of NH₄-N on water uptake in our studies was attributed to the NH₄ ion, in agreement with Quebedeaux and Ozbun (24), rather than to NH₃ as suggested by Stuart and Haddock (28) since solution pH under NH₄-N did not exceed pH 7.0.

Although water stress and leaf and root resistances to water flux were greater under NH₄ nutrition, solution uptake per fresh wt increase per week (Table 7) was increased by NH₄, implying that the reduction in tissue ion concn under NH₄-N was due primarily to nutritional rather than to water flux effects. Decreased water use efficiency with NH₄ nutrition has been observed previously (14).

Under NH₄-N, solution pH did not affect intact plant transpiration (Table 7) but did affect R_L (Table 6) suggesting that transpiration was controlled by nonleaf resistances. The increased transpiration rate of excised shoots of NH₄-fed plants at pH 6.5 was likely due to decreased R_L. Under NH₄-N, leaf resistance was lowest and root resistance highest at pH 6.5. It is possible that periodic adjustment of solution acidity gave greater NH₄ uptake and greater synthesis into organic compounds (3, 4) resulting in a more negative cellular osmotic

Table 8. Values initially and at time of solution replacement of solution pH and electrical conductivity.

N form		Initial values ^Z		Values at soln replacement ^Y	
		pH	EC (μmho cm ⁻¹)	pH	EC (μmho cm ⁻¹)
NO ₃	Control	4.52	2240	6.99a	3170b
	4.0	4.00	2310	7.04a	3051b
	6.5	6.50	2260	7.04a	3253b
NH ₄	Control	4.64	3840	3.42b	4369a
	4.0	4.00	3310	3.42b	4378a
	6.5	6.50	3840	3.50b	4451a

^ZMean of 36 determinations; conductivity by Yellow Springs Inst. Model 31 with YSI 3403 cell.

^YMean separation with columns by Duncan's multiple range test, 5% level.

potential. The ensuing less negative cellular turgor potential might then give a less negative ψ_p .

In contradiction to previous observations of reduced shoot NH₄ concn (3, 4, 8) with acidity control under NH₄-N, an increased shoot NH₄ concn was observed. This apparent contradiction may reflect short-lived acidity control in the low-buffered solutions. Increased NH₄-N uptake and/or increased deamination of the transport amino acids may have been involved also.

This study has shown that NH₄-nutrition resulted in fresh wt reductions because of both increased water stress and impaired ion uptake. Under NH₄-N, solution acidity control improved root growth and reduced plant water stress but was without effect on either total plant fresh wt or ion concn of roots and shoots with the exception of increased shoot NH₄-N concn.

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Cadmium and Zinc Toxicity in White Pine, Red Maple, and Norway Spruce¹

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Abstract. Excessive accumulation of Cd or Zn in white pine (*Pinus strobus* L.), red maple (*Acer rubrum* L.), and Norway spruce (*Picea abies* L.), resulted in reduced root initiation, poor development of root laterals, chlorosis, dwarfism, early leaf drop, wilting, and necrosis of current season's growth. Positive correlations existed between nutrient culture levels and tissue accumulation when plants were grown in sand. White pine seedlings accumulated more Cd and Zn than either red maple or Norway spruce when compared in similar experiments. White pine appeared to be more tolerant of Cd and Zn accumulation than either red maple or Norway spruce since visual phytotoxicity symptoms were observed only at the higher treatment levels. Accumulation of Cd and Zn from a medium of 2 sand: 1 soil: 1 perlite by volume was also observed.

The accumulation of heavy metals in trees is a factor which may contribute to stress in highway, commercial, and residential plantings. Positive correlations between heavy metal accumulation and proximity to highways has been demonstrated in areas of high traffic density (3, 9). The heavy metals cadmium and zinc could contribute to the stress of ornamental trees particularly in an urban environment.

The chemical and physical properties of Cd and Zn are similar and often sources of Cd and Zn are such that the two metals are inseparable in industrial grade chemicals. Both metals are released into the environment during the use or breakdown

of lubricating oils, vehicle tires, galvanized metals, and fertilizers (5, 8). In addition, waste water from mines, smelters, and sewage treatment centers are other sources which may ultimately contribute to soil contamination (1, 2, 4, 7, 10, 12).

This study was designed to determine concentrations of Cd and Zn in leaves, stems, and roots of 3 woody ornamentals in order to ascertain foliar levels for plants displaying visual toxicity symptoms.

Materials and Methods

Two or 3-year old seedlings of red maple, white pine, and Norway spruce were grown in fiberglass greenhouses under natural daylengths with day and night temp of 27° and 15°C, respectively. All plants were planted in 0.9 liter plastic containers in a medium of acid-washed sand and irrigated with Hoagland's nutrient solution (6), supplemented with either 0, 0.5, 1, 2, 4, 8, or 16 µg/liter Cd. White pine seedlings were also treated with 32 and 64 µg/liter Cd. All 3 species were similarly exposed to 0, 6.25, 25, 50, 100, 200 and 400 µg/liter Zn. All treatments were initiated by saturating the medium with the Cd-enriched nutrient solution after the new growth had

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