Ammonia/Ammonium Toxicity Root Symptoms Induced by Inorganic and Organic Fertilizers and Placement

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ABSTRACT

Ammoniacal fertilizers can cause seedling damage. The present aims were to characterize spatial and temporal, root morphological NH$_3$/NH$_4^+$ toxicity symptoms, assess the extent of the toxicity zone, and relate species-specific responses to their root architecture. Wheat (Triticum aestivum L.) and canola (Brassica napus L.) were exposed to seed and deep placed urea. Faba (Vicia faba L.) seedlings were grown above organic amendments. Time-sequential images of canola root apex and root hair die-back, discoloration, and accelerated lateral rooting were captured with soil-buried, high resolution digital scanners. Seed-placed urea stunted wheat shoot and root radicles, while slow-release urea allowed greater wheat seedling survival, while toxicity-damage to a single tap root of the germinating canola and faba often resulted in seedling mortality. Urea and chicken manure developed expanded NH$_3$/NH$_4^+$ toxicity zones 1.5 to 5 cm, eliciting similar toxicity symptoms initiated at the root apex. Within 3 d after planting, canola tap root elongation stopped, followed by progressive basal directed necrosis and shrinking of the root axis, root hairs. These characteristic symptoms may be used for future toxicity diagnostics of soil-grown plants. Elevated pH in the soil zone above the chicken manure suggested NH$_3$ gas transported through soil pores followed by H$^+$ consumption and elevated NH$_4^+$. Ammonia gas toxicity and species-specific root system architecture should be considered in N placement and source selection.

Core Ideas

• NH$_3$/NH$_4^+$ toxicity initiates at the root apex and moves basipetally.
• Symptoms include tissue discoloration, axis shrinkage, root hair disfigurement, and seedling death.
• Toxicity zones ranged from 1 to 5 cm from the ammonia sources.
• Putative upward movement of ammonia raised soil pH and NH$_4^+$ above chicken manure.
• Most wheat axes avoided NH$_3$/NH$_4^+$ toxicity zones, improving survival over tap-rooted species.

The negative impact of starter fertilizers in the inhibition of seed germination has been recognized since the 1920s (Millar and Mitchell, 1927), and awareness of potential toxicities of N fertilizers was magnified as synthetic ammoniacal fertilizers were widely adopted in the 1950s. Mechanisms of toxicity include salt toxicity and specific NH$_4^+$ toxicity, however, NH$_4^+$ toxicity has occurred at concentrations lower than can be explained by salt toxicity (Barker et al., 1970). Plants are particularly sensitive to high NH$_4^+$ environments during germination and early seedling development. Cooke (1962) first demonstrated that a NH$_3$ gas build-up during urea hydrolysis was primarily responsible for reduced seed germination and seedling root damage, and nitrite accumulation could be another cause (Oke, 1966). Other byproducts of urea fertilizers; that is, biuret and cyanate were dismissed as potential causal factors in favor of ammonia accumulation following urease catalyzed urea hydrolysis (Bremner and Krogmeier, 1989).

Much of the plant nutrition research has focused on NH$_4^+$ ion uptake and toxicity. Ammonium uptake is highly regulated by NH$_4^+$ transporters (Loque and von Wirén, 2004). Plant species vary in their sensitivity to NH$_4^+$ nutrition (Britto and Kronzucker, 2002; Dowling 1993; Brenner and Krogmeier, 1989), and genotypic variation within a species such as rice (Oryza sativa L.) has also been observed (Chen et al., 2013). Yet, some species variation in radicle vs. coleoptile sensitivity to NH$_4^+$ was not correlated to their germination sensitivity to NH$_4^+$ (Dowling, 1993). Ammonia gas was identified as the causal toxicity factor by suspending seedlings above a solution of NH$_4$OH. In terms of mechanisms and pathways of uptake, much more is known about NH$_4^+$ uptake compared to NH$_3$ (Miller and Cramer, 2005). The electroneutrality of NH$_3$ has suggested that membrane channels may be a pathway for NH$_3$ uptake (Howitt and Udvardi, 2000).

Symptoms of NH$_4^+$ toxicity include overall suppression of growth, leaf chlorosis, and reduction in root/shoot ratio with particular inhibition of fine roots (Britto and Kronzucker, 2002). Root symptoms have been described as “hollow interior of roots followed by discoloration and rotting” (Hoque et al., 2007). Ammonium sources cause inhibition of the root elongation and elevated rates of NH$_4^+$ efflux (Britto et al., 2001; Li et al., 2010; Chen et al., 2013). Inhibition of root elongation has

Abbreviations: PCU, polycoated urea.
been observed within 4 to 8 h of exposure of various Orobanche species to ammonium sulfate (Westwood and Foy, 1999).

Toxicity of NH$_4^+$ ions were found to be 100 times less toxic than neutral NH$_3$ to microalgae, Nephroselmis pyriformis, as determined by comparing EC50 levels required to elicit toxicity responses (Källqvist and Svensson, 2003). Ammonia toxicity has been associated with reduced tissue respiration of roots, perhaps due to disruption of membrane integrity (Vines andWedding, 1960). Solution-grown plants with ammoniacal-N forms in high solution pH have shown NH$_3$ sensitivity (Bennett and Adams, 1970; Gill and Reisenauer, 1993).

The correlation between NH$_3$ release of different sources of N fertilizers placed with the seed, and reduced seed germination lead to speculation that NH$_3$ gas was the causal toxic factor (Brage et al., 1960). A comparison of N sources revealed urea causes more corn root damage than diammonium phosphate or ammonium nitrate, due to higher pH shifts with urea causing a higher ratio of NH$_3$/NH$_4^+$ (Creamer and Fox, 1980). Similarly, banding full season rates of ammoniacal fertilizers, in or near the rice seed row, produces a high NH$_3$/NH$_4^+$ environment that is encountered by a germinating plant seedling. This resulted in reduced seed germination and root growth of surviving seedlings of direct-seeded rice (Qi et al., 2012). The banding of urea near the dry seeded rice seed row caused a 91% decrease in seed germination of one rice variety while ammonium sulfate had no effect, implicating volatile NH$_3$ ammonia as the toxic factor. Banding ammoniacal fertilizers 7 to 8 cm below the seed row of winter wheat caused reduced plant populations at several locations (McKenzie et al., 2001). Banding urea or urea-ammonium nitrate 2.5 cm below and 2.5 cm to the side of the seed row caused seedling damage and reduced stand density of spring canola, while adding a urease inhibitor significantly lessened these effects, and increased seed yields at some locations (Grant et al., 2010). A comparison of direct seed drills that placed N fertilizer in a side band to the seed row, canola stands were more adversely affected than wheat by increased N rates up to 120 kg N ha$^{-1}$ (Johnston et al., 2001). Reasons for this interspecies difference in NH$_4^+$ tolerance were not elucidated.

The NH$_3$/NH$_4^+$ toxicity syndrome is not restricted to inorganic fertilizers. Organic amendments were shown to adversely affect root respiration within 4 to 5 h (Vines andWedding, 1960). Adverse effects of organic nutrient sources on seed germination have correlated with the concentration of NH$_4^+$ in amendments, for example, chicken manure (Wong et al., 1983), while sources high in cation exchange capacity such as peat can help ameliorate the toxic effects of NH$_4^+$ relative to inorganic NH$_4^+$ sources, thereby improving root development at moderate rates of application (Abbès et al., 1995). Ammonia was also suggested to be a biotoxic causative factor in controlling Verticillium wilt (Verticillium dahliae) with organic amendments (Tenuta and Lazarovits, 2002).

Tremendous advances have occurred in the imaging and sensing of soil chemical-root interactions (Blossfeld et al., 2013; Santner et al., 2015). High resolution root imaging with inexpensive CCD flatbed scanners have advanced rhizotron-type imaging of developing root systems, whereby interspecies species variation in root hair density and lengths were discerned in response to soil conditions (Hammac et al., 2011). This technique was used in several experiments described herein to visualize root responses to organic and inorganic sources of NH$_3$/NH$_4^+$, with the objectives to characterize spatial and temporal toxicity symptoms, assess the extent of the toxicity zone, and relate species-specific toxicity severity to their root architecture.

**MATERIALS AND METHODS**

**Experimental Setups**

For scan series 1 and 3, flatbed scanners (Canon CanoScanLiDe700F scanners, Melville, NY) with 29.7 by 21.6 cm scanner faces were waterproof sealed with silicone glue and two scanners were placed inside a 36 by 34 by 24 cm (height by length by width) plastic container with inward facing scanner as described by Hammac et al. (2011). Scanners were seated on opposite sides of each containers facing inward at an angle of 20 degrees from vertical to encourage root growth along the scanner face (Hammac et al., 2011). Plexiglass scanner plates faced pre-moistened soil filled into the containers. Palouse silt loam (fine-silty, mixed, superactive, mesic Pachic Ultic Haploxeroll) was collected near Pullman, WA, and screened with 2 to 4 mm mesh sieve. Images were scanned at 118 pixels cm$^{-1}$ for full plate views of seeds, fertilizer prills and layers, shoot coleoptiles, root axes and lateral roots, with higher resolution imaging, up to 1890 pixels cm$^{-1}$, of root hairs and other areas of interest. In scanner scan series 2, a plexiglass box was fixed to the face of the flatbed scanners (Epson Perfection V37, Epson America, Long Beach, CA). The boxes were 18.5 h by 21.5 w by 7.5 d cm (width by height by thickness). A removable back panel was bolted to the side of the box opposite to the scanner to facilitate the packing of the box. All plants were grown under artificial lighting (400 mmol m$^{-2}$ s$^{-1}$) with a 16:8 h light/dark cycle, and canopy air temperature was maintained at 20°C.

**Scan Series 1: Wheat Responses to Seed and Deep Placed Urea and Polymer Coated Urea**

Spring wheat (cultivar Kelse) seeds were planted in two rows perpendicular to opposing scanner faces of each container, filled with Palouse silt loam with gravimetric moisture content adjusted to 250 g (kg soil$^{-1}$). The seed rows were 15.2 cm apart, 2.5-cm deep, and seeds were spaced 2.5 cm apart within each row. Fertilizer N band densities of each row within a container were 8, 17, and 25 mg N cm$^{-1}$, equivalent to 56, 112, and 168 kg N ha$^{-1}$, with one row fertilized with urea and the other row of the same container fertilized with polycoated urea (PCU). Each container set up was duplicated to produce four images of each combination of N rate by fertilizer form and placement. Both fertilizers were placed with the seed at 8, 17 mg N cm$^{-1}$, equivalent to 56 and 112 kg ha$^{-1}$, and separate paired containers had each fertilizer banded 5.2 cm below the seed row. The containers did not receive additional watering during the 8 d experiment.

Each group of four scanned seed/seedlings were subjected to unique combinations of two fertilizer forms, three N rates and two placement combinations, treated as replicates for analyzing radicle emergence differences among treatments using one-way analysis of variance at $p < 0.05$ of committing a type I error. Shoot emergence differences due to fertilizer form and
placement were grouped over N rates and statistically evaluated with one-way analysis of variance at \( p < 0.05 \).

**Scan Series 2: Canola Root Morphological Responses to Deep Placed Urea**

A preliminary experiment was first conducted with a single scanner facing soil divided between fertilized and unfertilized sections. A urea band of 19 mg N cm\(^{-1}\), equivalent to 90 kg ha\(^{-1}\) with 15 cm row spacing, was placed 7.5 cm below the surface of a Palouse silt loam, against and parallel to the scanner face. The soil was passed through a 2-mm sieve and wetted to 250 g water (kg\(^{-1}\) soil), prior to being packed into the growth boxes. Three seeds of spring canola (Dekalb cultivar 30-42) were placed against the scanner face 2.5 cm below the soil surface with or without a urea fertilizer band. The scanner was oriented parallel to seed row. Seedlings were allowed to grow without watering, and images were collected at 10 d into the experiment.

A second canola imaging experiment was conducted with the same soil to capture the time course of NH\(_3\)/NH\(_4\)\(^+\) toxicity symptom development. Three replicates of low and high fertilizer rates were established by banding the equivalent of 34 kg N ha\(^{-1}\) or 67 kg N ha\(^{-1}\) at 19 cm row spacing. These two fertilizer treatments were simulated by placing fertilizer bands of urea at 6 and 13 mg N cm\(^{-1}\) row 7.5 cm below the soil surface and 5 cm below the seed rows. The seed and fertilizer rows were placed perpendicular to the scanner face, providing a cross-sectional image of the seed row. The control treatment without a fertilizer band was replicated twice. A series of color scans at 1890 pixels cm\(^{-1}\) (4800 dpi) resolution and set to collect images every 4 h. The time stamp of capture was taken from each image to make the time line. Temporal and spatial measurements of toxicity symptoms were recorded. Root length and axis diameter measurements were made using the measure tool in ArcMap (ESRI ArcMap, measurement tool, Redlands, CA). The length measurements were made on the sequence of images and fitted into a time line describing symptom occurrence. Taproot shrinkage was defined as the incidence of greater than 20% shrinkage of the taproot axis diameter over time. Lateral root branch numbers were also recorded over time.

**Scan Series 3: Faba Bean Root Responses to Layered Organic Amendments**

Another taprooted species faba bean was subjected to organic amendments differing in ammonium concentration. Four replications of time-sequenced root images were captured by scanning faba bean roots growing in each of three soil treatments: (i) unamended Palouse silt loam soil throughout the container, (ii) an 11.4 cm layer of Palouse silt loam over a 5.1-cm organic layer of (ii) mature compost or (iii) chicken manure, over 11.1 cm of unamended Palouse silt loam. All containers were uniformly watered to 250 g (kg soil\(^{-1}\)) before planting. Five faba bean seeds were planted 4 cm apart along each scanner at a 4-cm depth. The experimental units were set up as described for scan series 1. Plastic wrap covering the soil minimized evaporation prior to plant emergence. Root scans were conducted every 24 h during the 25 d experiment.

**Soil Analysis**

Soil and organic amendment layers were sampled and analyzed prior to the experiment and again at the end of the experiment. Soil NO\(_3\) and exchangeable NH\(_4\) were extracted with 1.0 M KCl at 10:1 extractant/soil mass ratio, and quantified by modified flow injection analysis (Lachet Instruments, Quick Chem FIA model 8000, Milwaukee, WI) using color reagents salicylate-nitroprusside for ammonium detection, and sulfanilamide for nitrite detection following Cd-Cu reduction of nitrate (Hofer and Prokopy, 2001). Total N was determined by dry combustion analysis (Leco CN model 2000, Saint Joseph, MI). Soil pH and electrical conductivity were determined on a 1:1 soil/water (kg/kg) paste (Orion Research pH meter model 211, Waltham, MA; Spectrum ECTestr high+ EC meter, Aurora, IL).

**RESULTS AND DISCUSSION**

**Wheat Root Responses to Seed and Deep-Placed Urea and Polymer Coated Urea**

Urea dissolved within 2 to 3 d, while the PCU appeared to remain pelletized over the 8 d experiment. Proctor et al. (2010) has demonstrated that urea applied to soil or crop residues emit NH\(_3\) within 2 to 5 d of application. No roots survived seed-placed urea at either rate, while 75% of the seeds (\( p < 0.05 \)) produced viable, elongating radicles within 2 to 3 d with seed placed polycoated urea (PCU) at either rate (Fig. 1). Pathogen invasion of necrotic radicles resulting from seed placed urea was evidenced by the appearance of fungal hyphae within 5 to 7 d after planting. Shoot coleoptile development was inhibited 50% or more (\( p < 0.05 \)) by seed placed urea compared to seed placed PCU and deep banding of both sources.

![Fig. 1. Wheat seedlings germinated with seed-zone placed polymer-coated (A–C) urea pellets or (D–F) urea prills. (A,D) 5, (B,E) 6, and (C,F) 7 d after planting.](image-url)
Deep-placed urea fertilizer of both forms resulted in normal shoot and root initiation (Fig. 2). Wheat root seminal axes were observed to stop growing when axes grew within 2 cm of dissolving uncoated urea pellets (Fig. 2), and necrosis of the root tip discoloration evident (Fig. 3). Some seminal axes were able to grow directly into the PCU band and either grow past the pellets, possibly due to slow-release of NH$_3$/NH$_4^+$.

Interestingly, one root grew in between two pellets, and developed some apical discoloration and root hair disfigurement (Fig. 4), perhaps due to higher urea release from pellets on both sides of the apex, compared to the healthy root adjacent to only one pellet. In the meantime, other axes were able to grow around that zone to deeper depths (Fig. 2). Since wheat develops numerous seminal axes, the damage of one axis did not adversely affect shoot development. Yet root diseases can still be prevalent with deep fertilizer placement below or to the side of the seed row (Cook et al., 2000), possibly exacerbated in fertilizer-injured roots.
There was no difference between the rate at which shrinkage in the plants which had intercepted the fertilizer band (Fig. 7). Within 12 h of the cessation of apical growth tap roots were observed to begin girth shrinkage in an apical toward basipetal direction. The progression of the shrinkage was observed only in the plants which had intercepted the fertilizer band (Fig. 7). There was no difference between the rate at which shrinkage progressed in the low treatment (6 mg N cm⁻¹) or the high treatment (13 mg N cm⁻¹). The control did not exhibit apical to basipetal shriveling. In addition, premature emergence first order lateral roots then occurred within 24 h of the cessation of apical growth in canola plants subjected to both low and the high banded urea rates compared to control plants (Fig. 8). There were no sizable differences in the timing and rate of emergence between the two N treatments. Lateral emergence in the 0 N control appeared to be delayed in comparison to the high and low treatments.

Other qualitative symptoms observed, but not quantified were the dieback of root hairs along with root girth shrinkage and a browning of root tissue (Fig. 6). The progression of symptoms and modification of the seedling canola root architecture progressed in the low treatment (6 mg N cm⁻¹) or the high treatment (13 mg N cm⁻¹). The control did not exhibit apical to basipetal shriveling. In addition, premature emergence first order lateral roots then occurred within 24 h of the cessation of apical growth in canola plants subjected to both low and the high banded urea rates compared to control plants (Fig. 8). There were no sizable differences in the timing and rate of emergence between the two N treatments. Lateral emergence in the 0 N control appeared to be delayed in comparison to the high and low treatments.

In the second canola experiment repeated scans allowed for the sequence of toxicity symptoms to be observed. The symptoms of apical stunting, lateral branching, and apical toward basal shrinkage of the tap root (Fig. 6) as a result of fertilizer band encounter were observed on four roots with low fertilizer rates and four in high fertilizer rates. The cessation of apical growth occurred an average of 61 h after planting and at a mean distance of 13 and 18 mm from the initial fertilizer placement in the low and high treatments, respectively (Fig. 7 and 8). Within 12 h of the cessation of apical growth tap roots were observed to begin girth shrinkage in an apical toward basipetal direction. The progression of the shrinkage was observed only in the plants which had intercepted the fertilizer band (Fig. 7). There was no difference between the rate at which shrinkage

**Fig. 7. Time course of the canola taproot diameter shrinkage (>20%) from the root apex in a basipetal direction, following tap root growth termination after encountering 6 mg N cm⁻¹ or 13 mg N cm⁻¹ of row, 5 cm below a row of canola seeds placed 2.5 cm below the soil surface, compared to zero N control plants. Error bars represent standard errors of each treatment mean (± SE) at each time interval.**

**Fig. 8. First order lateral root initiation of canola following tap root growth termination after encountering 6 or 13 mg N cm⁻¹ of row, 5 cm below a row of canola seeds placed 2.5 cm below the soil surface, compared to zero N control plants. Error bars represent standard errors of each treatment mean (± SE) at each time interval.**

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**Canola Root Morphological Responses to Deep Placed Urea**

Scan series 2 experiments highlighted the susceptibility of canola, a tap rooted crop species to NH₃/NH₄⁺ toxicity via modified root architecture and physiological damage. Canola seedlings grown without a urea band placed below the seeds germinated and established strong tap roots which proceeded to grow to depths of 11.7 to 15.5 cm with first order lateral root extension by 10 d after planting (Fig. 5). In contrast, the taproots of the seedlings with deep banded urea ceased growing 1.7 to 1.2 cm above the urea band. Plants exposed to the urea band exhibited stunted apical growth, premature lateral roots, shrinkage of root width, and browning of the roots. Lateral emergence in the control plants occurred later and deeper than in the fertilized plants.

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**Fig. 6. (A and C) Canola root development in the high (13 mg N cm⁻¹) treatment and (B and D) the no urea control. At 49 h after planting roots in both the (A) treated and (B) control are healthy. By 110 h after planting the (C) high treatment shows stunted apical growth, shrinkage of root girth, lateral root emergence, disapearance of root hairs, and browning of root tissue in contrast with the (D) control which has continued to grow and mature out of the image frame.**
began within 24 h of the canola roots intercepting the fertilizer band, demonstrating rapidity with which NH₃/NH₄⁺ toxicity can modify root growth and architecture, and supporting the importance of considering fertilizer placement in agronomic planting operations.

**Faba Bean Root Responses to Layered Organic Amendments**

Ammonium-rich organic amendments are also capable of generating high NH₄⁺ levels and potentially eliciting NH₃ toxicity symptoms. Chicken litter applied to soil results in rapid NH₃ volatilization within 2 d of incorporation (Marshall et al., 1998). Initial compost and chicken manure layers had 12 and 1343 mg NH₄⁺-N kg⁻¹, and 2 and 50 mg NO₃⁻-N kg⁻¹, respectively (Table 1). Faba root growth was inhibited at the top of the compost layer (Fig. 9), with relatively little elevation in initial NH₃/NH₄⁺ migration into the above soil layer (Table 1). Presence of fungal hyphae and precipitate formation was apparent in and around the compost layer (Fig. 9), where pH ranged from 8.7 to 8.5 and EC ranged from 7.7 to 6.1 dS m⁻¹, indicative of excess soluble salts, including NO₃ potentially causing root growth inhibition (Del Pilar Cordovilla et al., 1999). In contrast, migration of NH₃/NH₄⁺ is indicated by greatly elevated levels of extractable NH₄⁺ in soil layers above and below the chicken manure layers, and concomitant increases in soil pH suggest the gaseous form migrated and neutralized H⁺ in forming NH₄⁺ (Table 1). This 5 cm soil zone of elevated NH₃/NH₄⁺ above the chicken manure band totally inhibited root penetration (Fig. 9), while roots penetrated to the bottom of the scan plate of the non-amended soil in which initial soil NH₃⁺ was 1 mg N kg⁻¹ and NO₃⁻ 50 mg N kg⁻¹ and these concentrations only slightly increased by the end of the 25 d experiment with soil organic matter mineralization (Table 1). Coupled with definitive solution culture evidence of the influence of alkaline pH enhancement of aqueous NH₃ concentrations and inhibition of root length (Bennett and Adams 1970), our root images and soil data imply that NH₃ upward diffusion and toxicity likely elicited the meristem blackening and root hair die back between Days 12 and 17 (Fig. 10).

**CONCLUSION**

The putative NH₃/NH₄⁺ toxicity zone affecting root development expanded 1 to 5 cm from the fertilizer sources. Given the rapid expansion of the toxicity zone in all experiments and the similar symptoms of root apex necrosis, we conclude that wheat, canola, and faba were all susceptible to NH₃/NH₄⁺ toxicity, likely resulting from NH₃ migration from the source. The most severe impacts on seedling health and viability occurred with the taproot species, canola and faba bean. In contrast, while band-intercepting wheat seminal axes were inhibited, most of the seminal axes effectively avoided the urea toxicity zone, which enabled more wheat seedlings to survive compared to the frequent lethal encounter of the single taprooted canola. A generation of commercial planters for direct seeding were designed with the capability of deep fertilizer placement for wheat production (Veseth et al., 1986). Yet the impact of this planter design on overall seedling health is likely

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**Table 1. Initial and final soil NH₄⁻-N, NO₃⁻-N, pH, and electrical conductivity (EC) of the soil and amendment layers of the three treatments: soil only, mid-layer compost, and mid-layer chicken manure. Differences (p < 0.05) between initial and final concentrations of the two N forms of each layer of the amendment treatments were designated by different letters.**

<table>
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<th>Treatment</th>
<th>Layer</th>
<th>Initial NH₄⁻-N</th>
<th>Final NH₄⁻-N</th>
<th>Initial NO₃⁻-N</th>
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<td>718b</td>
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more damaging to single taprooted crops such as canola than multiple-axis cereal crops, suggesting that different planting and fertilization strategies are necessary for direct seed canola production. We report the putative NH$_3$/NH$_4^+$ rich zones consistently arrested canola root growth and elicited a temporal progression of symptoms beginning with arrested canola tap root elongation, lateral root development, and sequentially followed by apparent root hair dieback, shrinkage of the root axial diameter, and root discoloration progressing from the apex to basal region of the main axis. Future soil fertility research should explore impacts of other ammoniacal fertilizer sources and identify placement alternatives of deep placed NH$_2$/NH$_4^+$ sources for tap-rooted crops. While much of the past physiological research has focused on NH$_4^+$ nutrition, more detailed root physiological research is needed to fully characterize the dynamics of NH$_4^+$ migration through soils and NH$_3$ uptake into root tissues. The specific visual root symptoms reported here may be useful in future field diagnosis of toxicities induced by concentrated synthetic and organic fertilizers.

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References


